Patterns of MAMMALIAN REPRODUCTION

S. A. Asdell, M.A., Ph.D.

PROFESSOR OF ANIMAL PHYSIOLOGY,
NEW YORK STATE COLLEGE OF AGRICULTURE,
CORNELL UNIVERSITY

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PREFACE

DURING the past few years several good books have appeared dealing with reproduction in general and with certain phases of it in particular. The approach has been that of the physiologist who wishes to synthesize; the books have dealt with functions and with the relations of functions to structures. With the advance in knowledge it has become apparent that reproductive phenomena, while depending upon similar basic principles in all species, fit together in diverse ways to produce the very varied patterns which constitute species differences. Recent work has tended to emphasize the importance of the quantitative aspects of reproduction. In our laboratory we have found that this method of approach has given us the explanation of several peculiarities in the estrous cycle of the cow, and it has enabled us to make certain generalizations upon hormone thresholds and reproductive patterns that are useful. Accordingly, it seemed to me that a beneficial purpose would be served if the available information on mammalian reproduction were brought together, species by species, with particular stress, wherever possible, on the quantitative aspects. I hope that this compilation will help lay the foundations of a physiological zoology of reproduction, so well begun by Dr. F. H. A. Marshall. The work involved has been heavy, but when I broached the subject to Dr. Carl Hartman his reaction was so encouraging that I undertook it; I could hardly do otherwise with his own example in the field to inspire me.

I have attempted to pick out the most important work for each species—that which would give some idea of the species' quantitative reactions—and to present the histological and physiological foundations upon which further progress in the subject may be built. The information available has been pieced together in as logical an order as possible, with occasional comment in the nature of comparisons or notations of inconsistencies in the data. I have indicated in places, especially in the introductions to each Order, certain

gaps in our knowledge, as suggestions to those who may have opportunities to carry on the work. Other problems will naturally suggest themselves if the abundance of knowledge regarding one species be compared with its dearth in another. I should like to point out here the comparative neglect from which the American fauna has suffered and to suggest that this is a field which might profitably be explored to the benefit of science and of the practical man, be he conservationist, pest controller, or animal breeder.

The literature is vast and widely scattered. I cannot fail to have made errors, but I hope that the sins of omission are more frequent than those of commission; the former do less harm in a work of this sort and can be more easily rectified. I trust that the book will be found sufficiently useful to warrant keeping it up to date. Accordingly, I shall be grateful if readers will draw my attention to papers containing material which should have been included. Most of the papers cited were read by me, but unless those in an unfamiliar language, e.g., Russian, were accompanied by an abstract in English, French, or German, this was impossible. In these cases I have relied entirely upon the information given in abstract journals. It is a pleasure to acknowledge the extensive use made of *Animal Breeding Abstracts* and *Biological Abstracts*. Dr. J. de Alba has helped me with the Spanish literature.

Others to whom grateful acknowledgments are due follow: Dr. S. E. Smith has read the section on Carnivora and Dr. S. L. Leonard that on Rodentia, and both have made useful suggestions. Dr. R. K. Enders has kindly given me access to his data on embryo counts in Central American species and has permitted me to use them. Miss Judith Churchill has helped in many ways, her critical ability having helped clear up several obscure passages in the first draft. Mrs. V. McCloskey has also put in many hours of careful work. Miss C. Sturtevant has undertaken the difficult task of editing the manuscript. Dr. Carl Hartman has read the entire manuscript and has made many valuable suggestions.

In picking out my references I have made no attempt to settle questions of priority; my choice has always been dictated by circumstances of completeness, seeming reliability, or of availability. All who have worked in the field are, in a sense, coauthors, and share responsibility for the book.

It has not been easy for me to pick my way among the pitfalls of zoological nomenclature, and, doubtless, this part is open to a good deal of criticism. I have tried to adhere to the best of modern methods of classification and to avoid duplication of species by bringing accounts given under various

specific names together into one fold. Unless there was physiological reason to do otherwise, subspecies were referred to only under the specific names. In several cases of doubt I have referred the matter of nomenclature to Dr. G. H. Tate of the American Museum of Natural History, and I am indebted to him for his help.

Many statistical data have been brought together and recalculated, and I have taken considerable trouble to indicate the degree of variability of such data. The probable error has been used throughout, together with the range within which about 80 per cent of the material falls. The mode, also, has been reported wherever possible, since the practical man is mainly interested in what happens most frequently and in the range within which the majority of observations may be expected to fall. Averages are useful for comparing species but not for use within a species. The counts of the number of young in most wild rodents are embryo counts.

When the amount of information relating to a species is insufficient for a separate article, the data have been given in tabular form. These tables come immediately after the articles relating to other members of the same family.

S. A. ASDELL

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PART I

THE SCAFFOLDING

INTRODUCTION

THE purpose of this chapter is not to give a detailed account of the physiology of reproduction but to give a summary which will help in understanding the information accumulated for each species of mammals. The patterns of reproduction, particularly of the estrous cycle, are many and varied. These variations have several causes. One lies in the variability of the output of sex hormones, including both the pituitary and gonadic hormones. This variability is shown in differences in the amounts produced and in the times at which the hormones are secreted. Another cause is expressed in the variation in threshold doses required to bring about changes in the "target" organs and in the differing sensitivity of the various tissues of the reproductive tract. A factor which has been appreciated all too little, but which is of great importance, is the influence of the central nervous system upon the output and action of sex hormones, particularly upon those of the pituitary gland. This is manifested in many ways, and, as knowledge accumulates, its far-reaching significance becomes more apparent. Environmental factors find their expression partly through the influence of nutrition and partly through that of light, especially, in the latter case, through changes in the amount of light to which an animal is exposed. The effects of temperature, surprisingly, appear to be small.

We believe that the prospects for progress in our knowledge of this field depend largely upon the development of these quantitative aspects of the subject. Our work has led us to believe that the output of the pituitary gland is related not only to the intensity of activity shown by the organs affected by its hormones, but also to the duration of hormonal action, and that these facts, together with the organ thresholds, explain many of the peculiarities inherent in a species. Thus, one of the main purposes of this book is to bring together the most significant and reliable quantitative data in order that a foundation may be laid for advances in this part of the field. As pure

hormones become available in sufficient amounts, we may confidently expect that these quantitative factors will be more fully explored. On the other hand, assays of circulating and excreted hormones in the normal animal are needed. At present this part of the field is in a state of much confusion due to a lack of agreement upon assay methods. Great help could be rendered by an authoritative work upon assay methods, by agreement upon their use, and by the adoption of standard methods of expressing results. At present too many kinds of units are in use, and their interrelations are altogether too vague. The results of biological tests vary with the species used, and with the strain when one species is employed. If, as seems almost inevitable, uniform strains cannot be adopted for assays, the strain employed should be stated and the relationship of assays upon that strain to those made upon a standard strain should be known. These suggestions seem obvious, but in reading through the mass of literature in which hormone effects have been given the writer has been appalled at the enormous amount he has been compelled to reject because he was unable to interpret the results in even approximate quantitative terms.

SEX DETERMINATION AND DIFFERENTIATION

Sex is determined by the genes carried in the chromosomes. In mammals the male is heterozygous, having but one X chromosome, and the female is homozygous, with two. This implies that spermatozoa are of two kinds, the X-bearer which will give rise to a female, and the Y-bearer which will give rise to a male. As these may be expected to be produced in equal numbers, the sex ratio at conception should be equality. This theoretical ratio is called the primary sex ratio, that at birth is the secondary sex ratio, and that at puberty is the tertiary ratio. The secondary sex ratio is rarely 50 per cent males; usually it is a little higher on the male side. As the sex ratio of abortions and of embryos is, in most species investigated, still more inclined toward the male side, sex ratio curves extrapolated to conception give a primary ratio in the neighborhood of 60 per cent males. This holds for pigs and man, but possibly is not so for the mouse. In all such work the assumption is made that the higher male mortality continues in the interval between fertilization and the time when the sex can be accurately diagnosed. Various attempts have been made to show that the Y-bearing spermatozoon is smaller than the X-bearer and so may be expected to travel to the egg faster. These have failed. If the two kinds of spermatozoa do have different rates of travel,

a high ratio of males may be expected when the spermatozoa are introduced into the female tract late, so that only a few reach the eggs before they are no longer capable of being fertilized. This is not the case according to the somewhat scanty data available. The higher mortality of males *in utero* has been ascribed to the possible effects of sex-linked lethal factors. The whole question is in an unsatisfactory state and needs further investigation. In pigs some information might be gleaned by a study of the sex ratio of the embryos in relation to their age and to the percentage of egg wastage which has already occurred. This study would require a fairly large body of data, but it could be carried out at a large packing house without much difficulty.

Attempts to modify the sex ratio by sorting out the two types of spermatozoa, using chemical or physical methods such as acid or alkaline media, magnetic fields, or centrifugation, have either failed or have yielded inconclusive results. A sex-linked lethal gene is known in horses which reduces the number of colts born to female "carriers" by half. The sex ratio of hybrids forms a special case, which is included in Haldane's rule: "When in the F_1 offspring of two different animal races one sex is absent, rare, or sterile, that sex is the heterozygous sex." Mammalian data amply confirm the rule.

There is a large gap in our knowledge of what happens between sex determination at fertilization and the first recognizable signs of sex differentiation. The gonads are represented at an early stage in embryonic development by two ridges on either side of the dorsal wall of the abdomen. In a prospective male one ingrowth of sex cords is produced as certain large cells derived from the yolk sac make their way into these germinal ridges. In prospective females the first ingrowth degenerates and is followed by a second which persists. Older workers held the view that these yolk sac cells were the precursors of the germ cells in the adult, but more recent views suggest that, especially in females, frequent renewal of the supply of germ cells is made from the germinal epithelium covering the gonad. However, it seems to be established that the male receives only the one ingrowth of the sex cords, and that the female receives two.

The question whether the somatic tissues are predetermined as to their sex or whether they are bivalent is not settled. There is bivalence in the sense that each embryo develops two sets of ducts: the Mullerian ducts, which give rise to the female internal accessory organs, and the Wolffian ducts, which give rise to those of the male. The external genitalia arise from the urogenital

sinus, which may undergo comparatively little differentiation, except internally, to produce the female external organs, or a good deal, to produce the male organs.

At present there is no embryological evidence in mammals that a male gonad can reverse to the female type, but such a change appears to be possible in the chicken. As the male gonad arises from the ingrowth of one set of sex cords, it is logical to conclude that true hermaphrodites (in which gonads of both sexes are present, either separate or mixed) and sex reversals cannot occur in genetic males but only in genetic females, where the first ingrowth may occasionally persist. If this view is correct, many of the so-called pseudohermaphrodites (in which the gonads are one sex and the accessory organs are mixed) are sex reversals. Evidence that this is sometimes so is contained in the sex ratio. The goat produces large numbers of this type of abnormality, and the sex ratio of strains producing them has a deficiency of females which may be rectified, at least in part, if the pseudohermaphrodites are regarded as genetic females. The sex ratio in cattle twins also becomes normal only if the freemartin is regarded as a female. Freemartins are apparently sex reversals, and their gonads are nearly always rudimentary testes. It is also significant that pseudohermaphrodites in which the gonadal tissue is ovarian are exceedingly rare. Some degree of persistence of the primary cords without degeneration of the secondary cords (true hermaphrodites), or with it (pseudohermaphrodites), is needed. Data on the sex ratio of families of pigs in which pseudohermaphroditism is frequent are too scanty for conclusions to be drawn.

It must be pointed out that pseudohermaphrodites in man do not fit into this scheme. Witschi has summarized information on the sex ratio in families in which the pseudohermaphroditic condition is hereditary and frequently occurs. Pseudohermaphrodites are evidently genetic males. This is borne out by the work of Severinghaus who investigated the chromosome complex in one such case and found both X and Y chromosomes. Chromosomal studies have not been made in the other cases cited. As some strains of goats produce many pseudohermaphrodites, the condition apparently being inherited as a simple recessive, its cytology and embryology could be worked out in this species fairly easily.

There is some indication that intersexuality arises in the offspring of fertile species hybrids, and it may thus be due to a disharmony in the quantitive factors which determine sex similar to that found by Goldschmidt in *Lymnantria,* the gypsy moth. This has been found in the second generation of

hybrids between two species of guinea pigs, *Cavia porcellus* x *C. aperea.* Most intersexes have been found in goats, pigs, and man, all of which as we know them at present may have originated in crosses of an interspecific order. In man the opportunity may have been somewhat remote, perhaps when Cro-Magnon and Neanderthal man existed. The question deserves further experimental investigation.

The freemartin needs comment. It occurs in cattle as a female cotwin to a bull calf. According to Lillie's view the condition is caused by anastomosis of the chorionic circulation early in embryonic life. This leads to the cross circulation of hormones from the developing gonad of the male and the suppression of growth of the secondary sex cords in the female. The resulting gonad somewhat resembles a testis, while the accessory organs, poorly developed, are mixed. Moore has critically reviewed the problem in the light of experimental sex transformation, in which, so far, it has not been found possible to produce the freemartin condition. Most of this work has been done on the rat and guinea pig. He also points out that similar anastomoses occur in pigs, in which a "partial" freemartin condition has been described (Hughes), and in cats, marmosets, and *Dasypus villosus,* in all of which it appears to be absent. It may be significant that the cow has the lowest known threshold of sex hormone activity; that the pig, in which the freemartin condition is only partial, has a higher threshold; and that there is evidence that the threshold in the cat is higher still. Accordingly, the ability to develop freemartins may be a question of the threshold which has to be exceeded before such action becomes possible. However, Moore doubts whether the embryonic gonad is capable of secreting any hormone at all at the time of the transformation.

The view that the soma is bipotential implies that circulating hormones can produce their effects wherever tissue is present which is capable of responding. The latter reservation is made because in normal development the Mullerian ducts respond, in the main, only to female hormones and the Wolffian ducts to male hormones. Action upon one set of ducts is accompanied by degeneration of the other set. Both kinds of ducts are present in the normal embryo of either sex. As a result it would appear that gynandromorphism (in mammals, the presence of a gonad and accessories of one sex on one side of the body and of those of the other sex on the other side) is theoretically impossible. However, such cases are known. The presence of both types of gonad should be followed by the development of both Mullerian and Wolffian ducts. One wonders what has become of the duct of the sex

opposite to the gonad on each side. An analogy is found in the normal bird, in which the oviduct does not develop on the side of the nonfunctional gonad. The condition is unexplained, but it may be significant that all cases of the kind which have been found so far are in rodents, one each in *Mus musculus, Microtus pennsylvanicus,* and *Cavia porcellus.* A similar distribution of the gonads has been found in *Bos taurus* and in *Sus scrofa,* in twenty cases altogether, but the accessory organs, except in one doubtful instance, do not conform to the gynandromorphic pattern. Is the tendency toward gynandromorphism one which has disappeared as the evolution of the reproductive tract has progressed?

The presence of testis tissue, either alone or as an ovotestis, tends to suppress the development of the oviduct, i.e., the top of the Mullerian duct, on the same side. Male accessories, i.e., the Wolffian duct, develop normally with an ovotestis on the same side, but if an ovary alone is present they suffer. In other words, the Mullerian duct suffers if the testis is near it even though it is supported by an ovary, but the Wolffian duct does not suffer from the ovary if a nearby testis supports it. Clearly there is a local influence which modifies development. It may be due to the earlier development of the testis. At one time the writer believed that this condition was peculiar to the Artiodactyla; now, however, he is not so sure, since cases in rodents may be interpreted similarly. In man the presence of both kinds of gonad in one individual usually causes the simple uterus to become bicornuate.

Apparent change of sex, caused by the circulation of sufficient quantities of the gonadic hormone of the opposite sex, occasionally happens after puberty. At this time the accessory organs are well established, and the structures that can respond are few. In the female the best indicator is the clitoris, which enlarges under the influence of androgens. A change of this nature which may be regarded as "essential" is found in the European mole. In the nonbreeding season the clitoris grows, and a mass of tissue above the ovary, resembling interstitial cells, enlarges. The clitoris of the guinea pig responds readily, under experimental conditions, when large amounts of estrogens are injected, or when gonadotrophes cause luteinization of the theca interna, a result which could hardly have been expected. In man similar changes are associated with tumors of the adrenal cortex and with certain tumors (arrhenoblastomata) of the ovary. The corresponding change in males is not so easy to detect. Perhaps human gynecomastics and milk-secreting male goats fall into this class.

PUBERTY AND SEXUAL MATURITY

At birth in some species, e.g., the guinea pig and man, the female tubular genitalia are in an active condition. Cornification of the vaginal epithelium or uterine bleeding may occur according to the species. The effect is transient and is believed to be due to the passage of hormones across the placenta from the mother. The condition has also been produced experimentally in some species, but not in others; and Courrier believes that it is only possible in species in which development is sufficiently far advanced at the time of birth. Thus, it has not been observed experimentally in rats and mice but can be made to occur in cats.

During the interval between birth and puberty the accessory organs respond to estrogens or to androgens, but the response of the gonads to gonadotrophes is variable. It is difficult to observe effects in the testes, so most work has been upon the ovaries, in which positive effects are more apparent. Species variations exist and are due to the stage of development of the ovary at the time of the experiment. In general, it seems that gonadotrophes do not hasten the development of female germ cells but do speed up their maturation. Thus, graafian follicles in a fairly advanced stage, possibly to antrum formation, are necessary before gonadotrophes can be effective. This aspect of the problem needs more work, and it is of practical importance as it may determine the value of gonadotrophic hormone injections during anestrum.

It is generally agreed that the attainment of puberty depends upon the release of gonadotrophes from the anterior pituitary since the injection of these substances causes it to occur prematurely. Also, infantile ovaries implanted in mature females rapidly mature, while mature ovaries implanted in immature females retrogress. Assays of the anterior pituitary reveal the presence of gonadotrophes well before the advent of puberty, but it is not clear whether the threshold is too high for a full response or whether an insufficient quantity is released. However, it should be remembered that gonadic development is a gradual process; the sudden increase in size of the ovary at the time of puberty is largely due to the copious secretion of liquor folliculi. The most striking instance of the gradualness is found in the higher primates in which the ovaries may, for some years, be sufficiently developed to cause the growth of body hair, sexual skin, and the mammary glands, while menstruation may be delayed for a time, and ovulation for a still greater time.

Puberty is not reached at the same proportion of mature body weight or of age at maturity in all species. In animals with a limited breeding season in each year it does not occur until that season is reached, and the young animals may then be almost fully grown. This is especially so in the carnivores. In animals with an extended breeding season, but with a winter pause in reproduction, those born late may have to wait longer than those born early enough to reach puberty in the same season. Completely polyestrous species vary in the proportion between their weight at puberty and that at maturity. Thus, in the meadow mouse, *Microtus pennsylvanicus*, puberty is reached at less than half the mature weight, a condition which is probably true for most polyestrous rodents, whereas in primates two thirds or more of the ultimate growth is made before the attainment of puberty.

The closeness of the fit of various factors with puberty has been studied in several species. Body length is least variable at this epoch, body weight next, and age the least constant. Under unfavorable conditions puberty is delayed, but if conditions are not too rigorous it is reached at a greater age, though at less body weight, than usual. Its attainment is due, therefore, not to one factor, but to several which interweave to produce the pattern inherent in the species. For example, the pituitary is early affected by undernutrition, and this, by depriving the gonads of stimulating hormones, affects sexual development.

As Crew has pointed out, puberty and sexual maturity are not the same. Puberty may be defined as the time at which reproduction first becomes possible, i.e., when germ cells are released. This definition separates the time of first heat and release of ova in rodents from the time of the opening of the vagina. However, on the average only about one day separates the two events; consequently, the discrepancy is not serious. In primates, menstruation without ovulation may occur for a while, but puberty is popularly regarded as the age at first menstruation, an epoch which is now referred to more precisely as the menarche. Sexual maturity is the time when the animal reaches its full reproductive power, and it is usually much later than puberty. Most animals which bear more than one young at a time are less fecund immediately after puberty than they are later. Thus yearling lambs usually have only one lamb when they are bred; later they have a higher proportion of twins and triplets. In rodents and pigs the first litter is usually comparatively small; the second litter is larger; and, following that, there is a small but regular increase until about the sixth, after which fecundity gradually declines, but at an increasing rate as the female gets older. Similar changes in

spermatogenesis are difficult to follow, but the available evidence indicates that they occur.

At this point the terms "fertility" and "fecundity" may conveniently be defined. Fertility is a qualitative term denoting the ability to produce young; fecundity is quantitative, denoting the number of young produced. Fertility is reached at puberty, but fecundity increases and decreases with age. Data are available from several species to show that early fertility and high initial fecundity are highly correlated with the lifetime performance of an individual. They form a good basis for economic selection.

THE HORMONES CONCERNED IN REPRODUCTION

The hormones concerned in reproduction are of two kinds, those which control the activity of the gonads and those which control the accessory sex organs. The first group are mainly derived from the anterior pituitary gland. They are three in number, Follicle Stimulator (F.S.H.), Luteinizer (L.H.) or Interstitial Cell Stimulator (I.C.S.H.), and Prolactin. The first of these, F.S.H., controls the growth of the graafian follicle in females and spermatogenesis in males. L.H. is necessary for the changes in the follicle which cause ovulation and the formation of the corpus luteum. In the male it is responsible for secretion by the interstitial cells of the testes. The third, prolactin, causes the cells of the corpus luteum to secrete. It is also necessary for lactation and appears to be the cause of the exhibition of maternal instincts, e.g., in rats, for retrieving the young and returning them to the nest. All these substances are proteins of the globulin or albumen group, and it is believed that they are secreted by the basophilic cells of the anterior pituitary. They are normally not excreted in the urine; but in man and, for limited periods, in the macaque and chimpanzee a substance appears in the urine during pregnancy with the properties of a mixture of the first two. It has also been reported in the urine of the pregnant giraffe. This substance is known variously as P.U. (Pregnancy Urine), A.P.L., Prolan, or Chorionic Gonadotrophin. In human males it appears in the urine if a chorioepithelioma is present. This fact and the high concentration in placental tissues lead to the belief that it is produced by the placenta. It is not known why its excretion in the urine should be limited to a few species. In the urine of women at the menopause or after they have been ovariectomized another substance with pure F.S.H. properties has been found. This is believed to be secreted by the anterior

pituitary. Its appearance in such large quantities without, apparently, affecting the ovaries, is a mystery since these organs are responsive to injected gonadotrophes at the menopause.

The blood serum of pregnant mares and asses contains a gonadotrophic hormone of placental origin which has the properties of a mixture of F.S.H. with a little L.H. This is known as Pregnant Mare Serum (P.M.S.) or as Equine Gonadotrophin. It is present for only a limited time, and it seems to be related to the somewhat unique reactions of the maternal and fetal gonads during pregnancy in the horse. This substance is not excreted in the urine.

The hormones secreted by the gonads mainly control the development of the accessory sex organs. They are steroids, derived from phenanthrene, and are closely allied chemically with the hormones of the adrenal cortex, some of which have similar physiological properties. The developing and mature graafian follicle produces estradiol, which causes the growth of the vaginal epithelium, producing keratinization of its superficial layers if it is present in sufficient quantity. It also maintains the uterine mucosa by causing capillary growth. Its action upon the cells of the uterine muscle is not yet clear —more work is needed upon its relation to their growth—, but it does increase their sensitivity and the amplitude of their contractions. This hormone also causes the growth of the duct system of the mammary gland and has some effect upon the growth of hair and the distribution of fat in man. It also hastens the ossification of the epiphyses of the bones, thus limiting the amount of growth after puberty has been reached. In large quantities it suppresses the activity of the anterior pituitary in forming F.S.H., and through this mechanism of reciprocal control ovulation is believed to be brought about. The suggestion is that secretion of F.S.H. is followed by that of L.H. By its action upon the central nervous system estradiol produces "heat" or the condition of receptivity to the male. Estrone, also, is present in the follicles.

The origin of estradiol is a subject of discussion. Some hold that it is secreted by the granulosa cells of the graafian follicles, but recent work has suggested that the theca interna cells produce it. This belief is more logical as it brings events in the ovary more in line with those in the testes. Knowledge of the estrogenic hormones stems from the pioneer work of Edgar Allen and Doisy.

The production of estrogenic hormones during pregnancy by the placenta is somewhat baffling, especially as the female does not come in heat at the time, but they have a well-defined function, which is, by action upon the anterior pituitary, to cause the maintenance of the corpus luteum. The hor-

mone progesterone produced by this body probably prevents the occurrence of heat.

Estradiol is not excreted as such, but is converted into other steroids with weaker estrogenic properties, estrone and estriol. In the mare it may be excreted in other forms as a series of these substances have been identified in the urine.

Progesterone, discovered by W. Allen and Corner, is secreted by the granulosa-derived cells of the corpus luteum. It causes the growth of the glandular system of the uterus and is essential for implantation of the embryos. As it maintains the endometrium, it is important for the continuance of pregnancy. It also causes the development of the alveolar system of the mammary gland. In a sense it is antagonistic to estradiol as it inhibits keratinization of the vaginal epithelium and reduces the sensitivity of the uterine muscle. It also prevents the rupture of graafian follicles, probably by limiting the production of L.H.

Progesterone is excreted in man and the chimpanzee as pregnandiol. This substance has not been found in the urine of any other species, so the fate of progesterone, except in man and chimpanzee, is unknown.

The corpus luteum also produces a hormone, relaxin, which, when it is secreted toward the end of pregnancy, causes the symphysis pubis to decalcify and relax, thus enlarging the diameter of the canal through which birth has to take place (Hisaw). This is the least explored of all the sex hormones, and its chemical nature has not yet been worked out.

Testosterone, discovered by Gallagher and Koch, is the only hormone known to be secreted by the testes. Its origin is in the interstitial cells, a fact which, long in dispute, has been proved indirectly by Courrier's work with the bat, and directly by Evans, who showed that it is produced by these cells when the hypophysectomized male is treated with L.H. It is excreted in a less potent form as androsterone. It causes the growth of, and maintains, the accessory male organs and possibly regulates the male distribution of the hair which appears in man at puberty. In deer it has some relation to the growth of antlers as these do not develop in an orderly way if the stag is castrated.

THE ESTROUS CYCLE

Some mammals breed at all times of the year; others have a more or less restricted season at a definite time of the year. In general, tropical species

have less restricted seasons than those living in temperate regions, but our knowledge of most tropical species is rather too scanty for adequate analysis. The season may begin at any time of the year, early spring for many rodents, late spring and early summer for Equidae, later summer and early fall for Caprinae, and early winter for Cervidae. Marshall has emphasized the fact that the season of the year is the determining factor since animals transferred from one hemisphere to the other soon adjust their habits to the reversed seasons, breeding at a different time of year, but in the right season, in their new environment. Much work has been done upon the causes of seasonal reproduction. Spring breeders, as has been shown by Bissonnette, may be caused to breed in winter if they are exposed to a longer duration of light each day. This effect is especially notable in the Mustelidae and the Canidae and is believed to be due to an influence of light upon the pituitary gland by way of the optic nerve. Fall breeders, i.e., species which breed at the time of diminishing light, do not give so clear a response to a lessening of their exposure to daylight. Goats may be induced to breed earlier by this method, but in sheep the results have been variable. In the latter species the situation is further confused because the strains with a long breeding season are those which have been produced in the more southerly regions near the Tropic of Cancer where seasonal changes in the length and intensity of light are not so great as they are farther north.

Another approach to this problem has been through the activity of pituitary gonadotrophes. The ovaries are responsive to these hormones in the nonbreeding (anestrous) season, so that the failure appears to be in the pituitary. However, these results have been somewhat conflicting, especially in sheep; threshold differences may exist and the condition of the ovaries at the time the injections were made may not have been sufficiently considered. It is reported that the amount of gonadotrophe in the sheep's pituitary is fairly constant throughout the year, but that it falls in the ground squirrel in anestrum. Naturally the content is not necessarily correlated with its rate of release, but sufficient data is available upon fluctuations in hormone level in different phases of the estrous cycle to indicate that the assay method is a promising approach to the problem. It has been neglected too long.

Some species, e.g., many of the Muridae, breed all the year in the laboratory but have a less extended season in the field. A factor which is important here is the food supply; reproduction is at a low ebb in winter and, often, at the height of summer, and the difference appears not to be related to temperature. Another fact is that, even in species with extended seasons, the intensity of

reproduction varies. Females of a wild species with a moderately restricted season tend to become pregnant at the beginning of the season, thus restricting the time in which breeding may be possible. This also tends to cause all females to be ready for a second breeding at about the same time, giving the appearance of two, or even more, restricted seasons in a year. This is especially apparent in the Sciuridae. An extended season with greater intensity at one time also tends to restrict the period of breeding, especially as young females breed better at the peak season. If the length of gestation is fairly great, approaching a year, this sets up a rhythm which is adhered to fairly closely. The bison, which has a very extended season if breeding is not allowed, but which had a well-defined season in the wild state, is an example of this tendency. Reports of limited seasons obtained from observations made upon animals in the wild state must, therefore, be considered from this point of view.

The females of some species ovulate only after the stimulus of coitus, but most ovulate spontaneously at regular intervals. The list of those which require stimulating is small at present, but it is expanding. Stimulation is probably the rule in Lagomorpha (rabbits), in many Sciuridae, Felidae, and Mustelidae, and in some Soricidae. It is thus not confined to any one Order. In these species the graafian follicle increases to a certain size at which it remains for a long period, 10 days to a month or more, during which the female remains in heat. Coitus, either once, as in the cat, or several times, as in the short-tailed shrew, causes the pituitary to release a gonadotrophic hormone which induces the secretion of more liquor folliculi, rapid growth of the follicle, and its rupture. This occurs at a fairly definite time after coitus, 10½ hours in the rabbit and longer in other species. Sometimes sexual excitement, or mounting by other females, is sufficient stimulus to evoke the reaction, which, therefore, depends upon the central nervous system and not upon nervous connections between the sexual organs and the pituitary. In the cat stimulation of the cervix uteri elicits the reaction, but it is not clear whether this is due to general excitement or to the local stimulus. This type of stimulation is insufficient in the rabbit.

As this reaction is clear-cut, it provided means by which the activity of the graafian follicle and the corpus luteum, which develops after the follicle has ruptured, could be differentiated. By the work of Ancel and Bouin much was learned of the physiological action of estrogens and of progesterone before active extracts of these substances had been obtained. The definite timing of ovulation has enabled the embryologist to obtain very accurately dated

material, and it has thus helped his work. In the rabbit copulation with a vasectomized or sterile buck is as effective as normal coitus in causing ovulation; consequently, by combining this technic with artificial insemination at known intervals, Hammond was able to learn much regarding the duration of fertility in the spermatozoon and the ovum.

In animals which ovulate spontaneously heat lasts for a varying length of time, and it is accompanied by the growth of the graafian follicle and ovulation. As the follicle secretes the hormone which causes heat, ovulation bears a fairly definite relationship to its cessation. The spacing of heats depends upon two factors. In one group of animals, i.e., in many rodents, ovulation is followed by the formation of corpora lutea which are not functional. In these animals the interval is very short, about 4 days, and it represents the time taken for the growth of a new wave of graafian follicles. In other species, e.g., in cattle and guinea pigs, the corpora lutea are immediately functional and the interval is longer, depending upon the time taken for their growth, the duration of their life, and the growth of new follicles. The decline of the corpora lutea and the growth of new follicles may overlap to some extent. The corpus luteum has a fairly definite length of growth and of life, about 10 to 14 days in most species. In a few, such as the pig and cattle, it lasts longer, from 16 to 18 days.

The corpora lutea of those species in which these organs are normally nonfunctional may be activated and rendered secretory by coitus with a sterile buck or by mechanical stimulation of the cervix uteri. The reaction is also produced in females which copulate but which do not become pregnant. Under these circumstances the corpora lutea last for 10 to 14 days, and the heat periods are separated by this length of time; the cycle becomes strictly comparable with those in which the corpora lutea are normally immediately functional. The condition has been called "pseudopregnancy," a name which has confused the recognition of the true nature of this modification of the cycle. Coitus provides sufficient stimulation to produce the effect even though the sympathetic chain connecting the reproductive tract is severed, but under these circumstances mechanical stimulation is ineffective. Apparently coitus can act by general stimulation of the central nervous system, but mechanical stimulus requires a nervous pathway from the reproductive tract.

It has been mentioned that the cessation of heat, and hence, to an extent, its duration, depends upon the time of ovulation. This is especially true in species with induced ovulation, for sexual receptivity ceases within a short time of that event. In females with spontaneous ovulation receptivity lasts

for a time that is fairly definite for the species, but only while fairly large follicles are present. The known exceptions are many bats, in which heat and ovulation are dissociated by several months, and the higher primates, in which receptivity is apparent at almost any time of the cycle.

Recent work suggests that the length of the heat period is related to several other quantitative factors. Certain species may be arranged in the order of the F.S.H. content of the anterior pituitary as follows: man, horse, pig, sheep, cow. In the order of the average length of the preovulatory or heat period the sequence is the same. The mean threshold of estrogens which maintains the reproductive tract or which causes receptivity in the ovariectomized female is in the descending order: horse, man, sheep, cow. Their order in regard to the excretion of estrogens each 24 hours is: horse, man, pig, cow. The inference is that the level of F.S.H. in the anterior pituitary is the pacemaker and that the patterns of heat, estrogen threshold, and output are related to it. It will be interesting to see, as further data become available, whether other species fit into this scheme and what effect differences in size may have upon their relative positions.

A factor in the length of the heat period is the development of a refractory state in the central nervous system. Zuckerman has shown in rats that the daily injection of estrogens into ovariectomized females at just above the minimal threshold dose for inducing heat causes a periodic heat of about the usual duration and at the usual interval. Evidently the animal becomes refractory to the hormone, and this period has to pass before heat is again possible. These results were deduced by a study of the vaginal smears. In the cow similar results have been obtained with sexual receptivity as the criterion of heat, and it is this fact which leads one to believe that the central nervous system is involved. Very large doses of estrogens have to be injected into the cow to induce continuous heat. In the cow this refractory period is apparently the cause of a dissociation between heat and ovulation, which occurs about 14 hours after psychic heat has passed off. The threshold is so low that it is reached comparatively early in the development of the graafian follicle; then, after the cow has been in heat for about 13 hours, the refractory period sets in before the follicle is ready to rupture. This is the only species in which ovulation has been found to occur regularly after heat has ceased except in certain vespertilionid bats which breed in the fall and which do not ovulate until the spring. The condition of the reproductive tract of the bat in the intervening time is described as one of subdued estrus (Wimsatt). It has not been fully determined whether another full heat occurs in

the spring, but the fact that in these species spermatozoa are found in the epididymis in the spring suggests that another may be possible. Further implications of this type of work are discussed in the section dealing with the length of life of the spermatozoa.

In the early stages of the growth of the follicles the ova grow more rapidly than the follicles themselves. As soon as the former reach almost their maximum size, their growth slackens and the follicles grow much more rapidly. Thus, as Parkes has shown, the preovulatory maturation of the follicle is not associated with further growth of the ova. These bodies enter a period of nuclear activity connected with reduction division and the extrusion of the first polar body. This activity usually precedes ovulation, but in many of the Canidae the first polar body is not extruded until the ova have been expelled from the follicles.

The factors which determine the length of life of the corpus luteum, and hence of the interval between heats, have not been studied in detail. The life of these bodies can be lengthened by the injection of estrogens, but, while estrogens may be the cause of the prolonged life of the corpora lutea in pregnancy, their influence on the normal cycle has not been demonstrated, and the level of circulating estrogens at this time is low. In the writer's opinion the life of the corpus luteum is related to the prolactin level in the anterior pituitary. When this is high, the corpora lutea persist for longer than usual. Thus, they persist in the cow for 3 to 4 days longer than the usual maximum in mammals, and the prolactin content of the anterior pituitary is high, as Turner has shown. In addition, in the smaller Muridae heavy lactation is associated with activation of the corpora lutea which are produced as a result of the post partum ovulation. This is associated with a higher lactogen content of the pituitary than occurs at other times in the cycle. The deduction is logical in view of work by Evans and by Astwood showing that prolactin is essential for the functioning of the corpus luteum, but it is not always possible to dissociate cause and effect until a problem has been very fully explored.

The accessory reproductive organs of the female come under the influence, often alternately, of two sets of hormones, estrogens and progesterone. Estrogens cause an increase of vascularity throughout the tract, a growth in the height of the uterine mucosa and of its epithelium, growth of uterine muscle cells, and rapid multiplication of the layers of cells in the vaginal epithelium. The latter proceeds so rapidly in some species that the superfi-

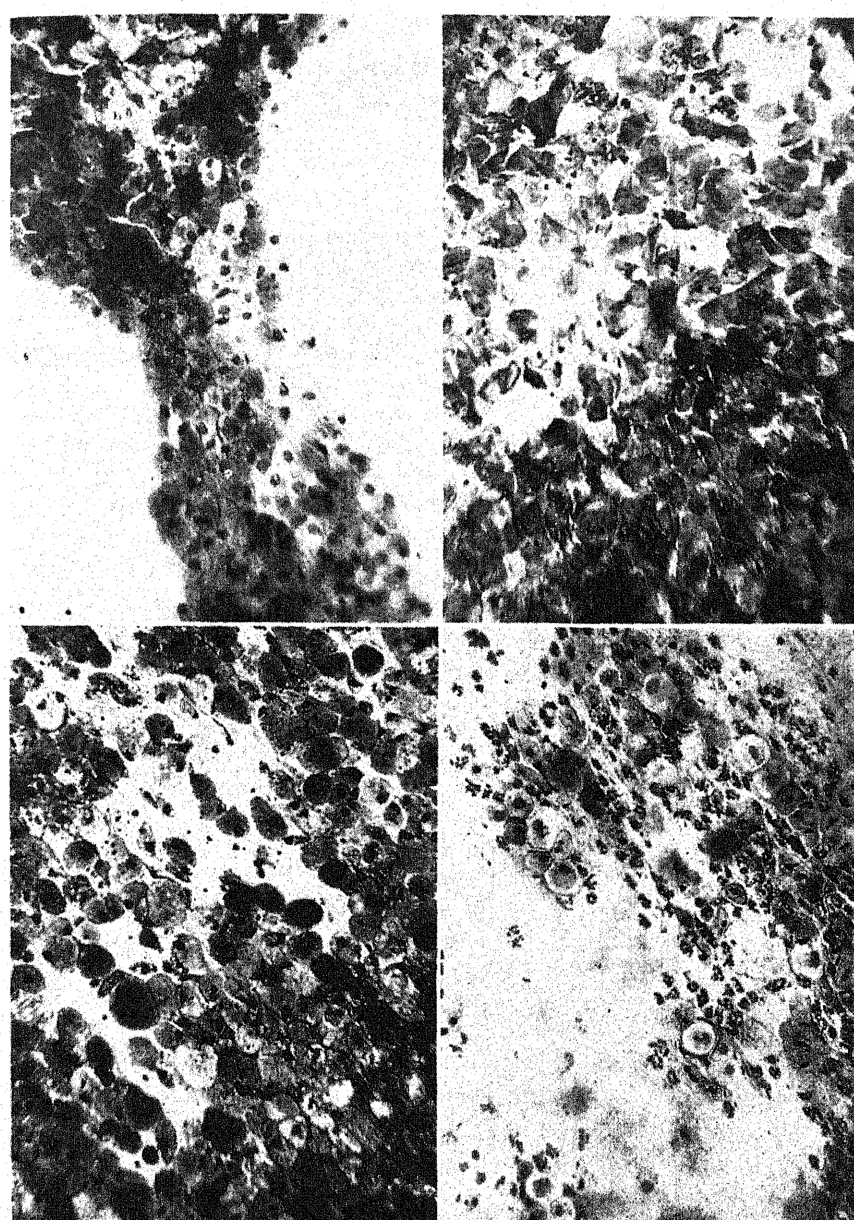

PLATE I. Vaginal smears of a guinea pig. *Upper left:* Proestrum, stage Ia, epithelial cells and cornified cells, H and E. x100. *Upper right:* Estrus, stage Ib, cornified cells, H and E. x100. *Lower left:* Estrus, stage II, round cells, H and E. x100. *Lower right:* Metestrum, stage III, epithelial cells and leucocytes, H and E. x100.

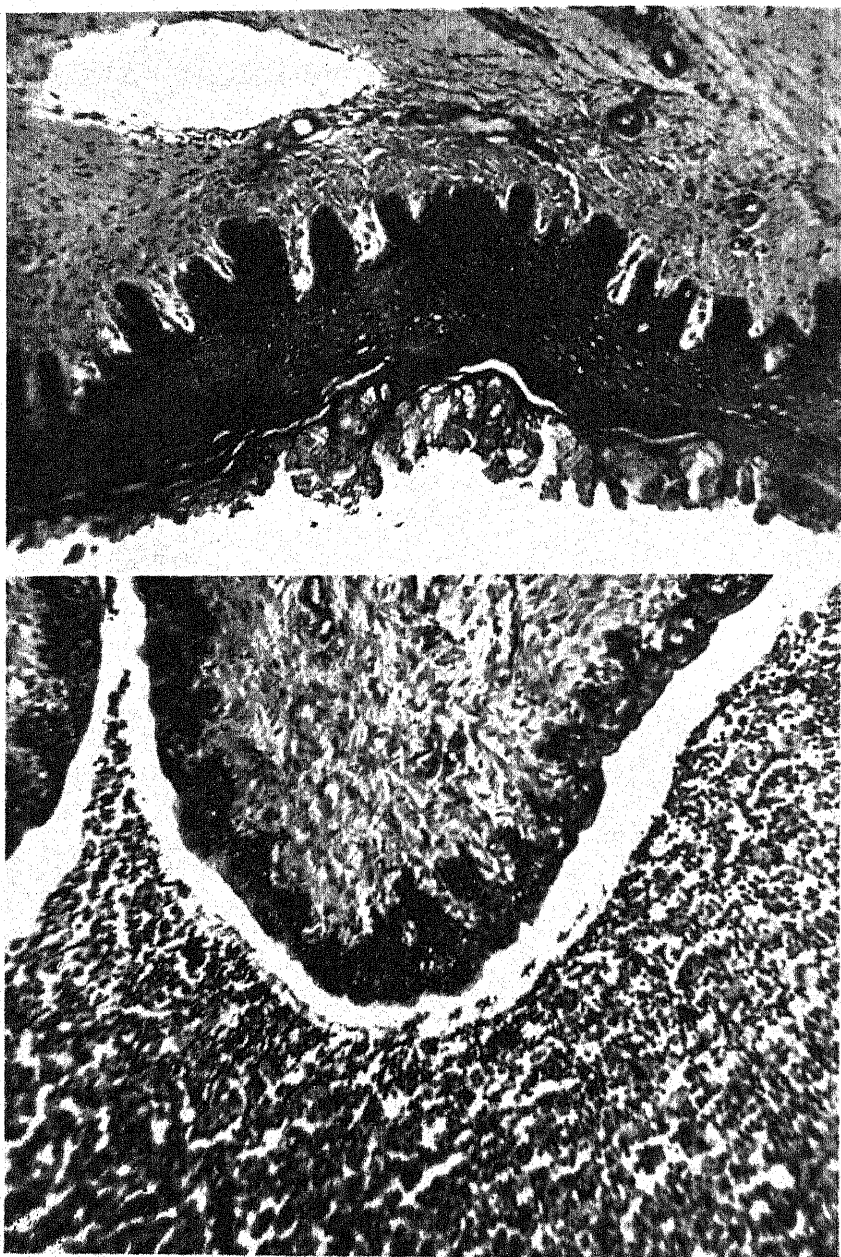

PLATE II. Vagina of a guinea pig, cornifying type of change with cycle. *Top:* Time of maximal growth. Note cornification. H and E. x100. *Bottom:* Time of desquamation. Note leucocytes. H and E. x100.

cial layers, at some distance from the blood supply, become keratinized. These vaginal changes are well marked in rodents generally and in the Canidae. In many other species similar changes occur but they are not so clearly defined. These changes are reflected in the vaginal smear, which consists largely of nucleated epithelial cells in the stages preparatory to and early in heat, and which changes to cornified cells near the time of ovulation. Then, with a lessening of the amount of circulating estrogen, degenerative changes set in, desquamation becomes massive, and leucocytes infiltrate. Between heats the smear is scanty and is a mixture of cell types together with a few leucocytes. In some species, of which the cow is an example, the circulating estrogen is so low, or the threshold is so high in relation to it, that cornification does not occur, but the superficial layers of the vaginal epithelium become tall mucus-secreting cells. In these forms cell types in the vaginal smear are not of much diagnostic value, but cyclic variations in the amount and consistency of the mucus can be followed. The injection of large amounts of estrogen causes keratinization of this type of epithelium.

Changes in the oviducts induced by estrogens are similar to those of the uterine epithelium.

Progesterone exerts its action mainly upon the uterus by causing the growth of uterine glands and by sensitizing the endometrium so that it produces deciduomatous tissue if it is irritated. The ovulated follicle takes 3 to 4 days to develop into a fully functional corpus luteum producing enough progesterone to elicit this effect. When it is fully formed, the corpus luteum continues to secrete sufficient hormone for about 4 to 6 days in the normal cycle. Another important effect of progesterone is to prevent the further development of graafian follicles, probably by a regulatory effect upon the anterior pituitary. These effects are definitely conducive to the early development, reception, and later development of the fertilized ova. They are also protective in that heats and coitus during pregnancy are prevented.

Many years ago Heape devised a series of terms for the different patterns of estrous cycles and for their component parts. The usefulness of these terms is not so great as formerly since we are now able in many cases to define the parts of the cycle as "estrogenic" or "progestational," depending upon the hormone which is effective at the time. However, they have their uses, especially in species in which the hormonal relations have not been fully worked out. In some instances, especially in the Muridae, confusion has

arisen by the use of Heape's terminology. It is not always clear whether a writer means the short or long cycle interval when he refers to the metestrum or diestrum.

In Heape's terminology the sequence of events from the growth of the follicle to the end of the life of the corpus luteum or to a new growth of follicles is called the "diestrous" cycle. When heat and its associated phenomena, including corpus luteum formation, occur as an isolated event, the species is monestrous; if series of cycles follow one another, it is polyestrous. A species is seasonally polyestrous if the females experience several diestrous cycles during a restricted part of the year. In monestrous and seasonally polyestrous species the period of sexual quiescence between seasons is termed the "anestrum." Proestrum is the period during which the follicles grow and the accessory organs are in a state of preparatory development. It is, therefore, the stage of mounting estrogenic activity. In monestrous females, such as the dog and deer, this stage is purely estrogenic; in polyestrous species it consists of a mixed, declining progestational and developing estrogenic phase. This is clearly seen in the cow, in which, at this time, the uterine muscle has a diphasic response to epinephrin. Proestrum is followed by estrus or the period of heat. During this period the estrogenic effects are at their height because of the rapid development of the follicles. Recent work distinguishes between the psychic estrus, or sexual receptivity, and vaginal estrus, or the time in which the growth changes in the vagina are at a maximum. The former period is usually the shorter.

If heat is not followed by the production of an active corpus luteum, the ensuing period in which sexual activity declines is called "metestrum." If a corpus luteum is formed, the female may be pregnant or pseudopregnant (a term denoting the activity of the corpus luteum following induced ovulation or activation) or she may enter "diestrum," the period in which the corpus luteum is active after spontaneous ovulation. In all three of these phases the reproductive tract is under the influence of progesterone. The writer would like to confine the term "metestrum" to the time during which estrogenic activity is declining and "diestrum" to the period in which the activity of the corpus luteum is paramount. This plan has been followed to some extent in this book, but, to avoid confusion, most dating in the metestrous and diestrous periods has been made as so many hours or days "postestrum," without indicating whether metestrum or diestrum, in the sense in which these terms are now defined, is meant. The rat cycle in which the corpora lutea are inactive consists, therefore, of proestrum, estrus, and

metestrum merging into proestrum. The cycle with an active corpus luteum consists of proestrum, estrus, metestrum, and diestrum merging into proestrum.

The nature of the primate cycle has received much attention, both because of its relation to human affairs and because of the well-marked division caused by menstruation, or the period of blood flow. This phenomenon is best observed in Old World monkeys; in New World monkeys, when it occurs, menstruation is confined to the appearance in the vaginal lavage of a few red blood cells, which can be picked up only by miscroscopic examination. Another difficulty in interpreting the cycle is the absence of a well-defined period of estrus, either psychic or vaginal. Coitus is permitted at almost any stage, but work with the chimpanzee has shown that it is most frequent at the time during which ovulation is probably occurring. In the New World monkeys there is some evidence that, as a rule, copulation is permitted only during a more restricted part of the cycle than in the Old World primates, but much more work needs to be done with the former species before certainty can be reached. The sequence of events in primates is as follows: After menstruation there is a period in which the uterus is repaired and then built up under the influence of estrogens, with growth of the endometrium and of its capillaries. The graafian follicle is growing and it ruptures near the mid-cycle, about 15 days before the beginning of the next menstruation. This is known as the stage of proliferation, and it is equivalent to proestrum and estrus in other mammals. It is accompanied by growth of the vaginal epithelium and some cornification, but these changes are gradual and not as well defined as they are in many other mammals. The vaginal smear is, therefore, of little help, though there are indications that more live leucocytes and more mucus are found in the smear about the time of ovulation. Ovulation is spontaneous, and it is followed by the formation of a corpus luteum, which causes great glandular growth in the uterus. This is called the "progestational" phase, and it is equivalent to diestrum in other mammals. The corpus luteum declines precipitously about 14 days after ovulation, and the more superficial capillaries in the endometrium collapse. Blood is extravasated in quantity, and about two thirds of the endometrium is desquamated.

A considerable amount of research has been done upon the cause of the uterine desquamation and hemorrhage. Some of this work has led to the enunciation of the "estrogen withdrawal" theory which, with modifications, is the basis of present explanations of the phenomenon. Edgar Allen found

that the endometrium grows and is maintained if estrogens are injected into ovariectomized rhesus monkeys. Continued injections do not cause menstruation, but if they are stopped endometrial desquamation follows after 7 to 10 days. It also follows bilateral ovariectomy at any stage of the cycle. As some workers have found a secondary peak of estrogen excretion just before menstruation, it was held that the latter is caused by the depletion of estrogens in the body, and hence the withdrawal of the growth stimulus given by them. However, the estrogen-induced growth is of the proliferative type only, and more recent work has shown that estrogen-withdrawal bleeding does not occur if estrogen injections are immediately followed by the injection of progesterone. This causes further progestational growth of the kind found in the primate diestrum. Cessation of progesterone injection is followed by bleeding. It therefore appears that the cessation of any growth stimulus to the primate uterus is followed by endometrial destruction and hemorrhage. Normal menstruation, therefore, is a "progesterone withdrawal" bleeding. Estrogen withdrawal may be indirectly involved since this substance is known to prolong the life of the corpus luteum. In some monkeys the sexual skin, which is highly edematous under the influence of estrogens, subsides a few days before menstruation, showing that estrogens are active during diestrum and that this activity ceases a little before menstruation, at the time when estrogens are excreted in quantity. This excretion may terminate the life of the corpus luteum, thus causing progesterone withdrawal.

Some women experience a little hemorrhage at the time that ovulation is believed to occur, and, as there is a second peak of estrogen excretion at this time, it is tempting to believe that the hemorrhage is associated with this peak and that the former is due to a brief interval before the progesterone influence makes itself felt. However, Hartman has shown that in rhesus monkeys bleeding of microscopic proportions is normal at this time and that it is caused by the rupture of highly congested uterine blood vessels, with little or no tissue destruction. It is also associated more closely with the presence of large follicles than with their rupture and is, therefore, believed to be a proestrous hemorrhage similar to that found in the dog.

The problem has been complicated by the existence of anovulatory cycles, principally in adolescent females. These are accompanied by menstruation, but the intervals are more irregular than they are when ovulation has become well established. Bleeding occurs from a proliferative (estrogen), and not from a progestational (progesterone), endometrium. This appears to be

a true estrogen-withdrawal bleeding caused by the atresia of follicles which did not receive sufficient gonadotrophic stimulus to cause them to ovulate.

Much effort has been spent in attempts to relate menstruation in primates with the periodic bleedings which are found in certain other mammals. But the times at which these occur do not lend support to any such relationship, and their nature seems to be different. Bleeding in lower mammals is more in the nature of seepage of blood unaccompanied by the destruction of tissue. This difference may, however, be one only of degree, though the bleeding is fairly copious both in the dog and the cow. The discharge of blood in the dog takes place during the proestrum, when the only ovarian structure to which it is likely to be related is the developing follicle. Meyer and Saiki have shown experimentally that the uterine growth following estrogen injections into ovariectomized bitches is accompanied by bleeding, which ceases when injections are stopped. It is, therefore, associated with excessive congestion. Of the Canidae only those of the genus *Canis* bleed during the proestrum. Occasional slight hemorrhage has been described in the bitch at the end of diestrum, or pseudopregnancy, and this may be a progesterone-withdrawal phenomenon. Van der Horst and Gillman have described intense, but localized, tissue destruction and hemorrhage in the uterus of the insectivore *Elephantulus myurus* at the end of diestrum, and occasional reports have suggested that it may occur in other insectivores, especially in those which appear to occupy an intermediate position between this group and the primates. The cow bleeds in metestrum, about 14 hours after ovulation. This does not occur invariably, and it appears more frequently in young than in old cows. Estrogen injections or withdrawal do not produce it, and, so far, its cause has not been found experimentally. Hammond believes that it is the result of a gap between the loss of function by an old corpus luteum and secretion by a new one, but progesterone-withdrawal symptoms in the uterine muscle are found in proestrum. Sometimes congestion is so great in the upper part of the vagina at proestrum that a little bleeding results. Microscopic bleeding from the uterus at about 8 days postestrum has also been reported by several observers, and its cause is unknown. Metestrous bleeding is also found occasionally in the guinea pig.

To sum up the work on the estrous cycle it may be said that, in its general pattern, it consists of the successive action of two groups of ovarian hormones, estrogens and progesterone. The relative length and intensity of its parts depend upon species thresholds and amount of circulating hormones, and also, in some species, upon the reaction of the central nervous system

to these hormones. Cycle lengths and the duration of their parts are not constant, but they may be expressed in averages for each species. Within species which have long heat or preovulatory periods calculation of the coefficients of variation has shown that this part of the cycle is the more variable in its length. In other words, the follicle takes a variable time for growth or to reach the stage of maturity required for ovulation, whereas the life of the corpus luteum is relatively constant. This, however, does not hold for the rhesus monkey.

The minimum time for growth of the follicle in the adult female is 3 to 4 days, which is the length of the interval in the rat and mouse and the time taken for heat to appear in the cow whose corpus luteum has been excised. The duration of heat depends upon the amount of F.S.H. produced by the pituitary, upon estrogen thresholds, and upon the length of time the central nervous system is capable of responding at a certain hormone level. Ovulation depends upon the release of L.H. by the anterior pituitary, and the duration of the corpus luteum upon the level of prolactin secreted. The role of estrogens in controlling the length of life of the corpus luteum is not clear except, perhaps, for its persistence during pregnancy. The change of secretion by the anterior pituitary which leads to ovulation is believed to be due to a reciprocal relation between the ripe follicle and the pituitary. Secretion of F.S.H. leads to estrogen secretion. The latter, as has been shown experimentally, causes F.S.H. secretion to cease, and it has been suggested that it is followed by the secretion of L.H. Perhaps careful pituitary assays in those bats in which heat and ovulation are dissociated might throw further light upon this problem.

Evidence is accumulating which shows that, in many species, luteinization of the follicular cells has begun before ovulation occurs. In this connection it may be recalled that Young showed that, in some species, a mixture of estrogen and progesterone is more effective in producing psychic heat than estrogens alone. This is a phenomenon which needs further study.

The patterns of response to estrogens have now been considered, but those to progesterone have not received enough attention. The Muridae in diestrum have little glandular growth in the uterus, but rabbits, cats, ferrets, and primates show great glandular growth and distension which give the endometrium a lacelike appearance. In general, this extreme reaction appears in species with induced ovulation and in primates, but the data are insufficient to stress the point. Other species than those mentioned appear to occupy an

intermediate position. A constant feature of progesterone action upon the glands is the high degree of coiling which is associated with their growth.

PREGNANCY

The most interesting feature of pregnancy to the endocrinologist is the persistence of the corpus luteum beyond the time found in the normal cycle. The work of W. M. Allen has shown that this is probably due to the influence of estrogens produced by the placenta. The cyclical length of the corpus luteum is sufficient to permit the developing egg to reach the stage at which implantation is possible and to maintain uterine sensitivity long enough for implantation to occur. After that the placental tissue, by producing estrogens, is able to prolong the life of the corpus luteum, but its persistence is not essential in all species. Its early removal probably always results in failure of implantation. After implantation occurs, the operation always results in resorption of the embryo or abortion in certain species, e.g., in the cow, goat, mouse, rabbit, ground squirrel, and possibly the dog. In man, monkey, guinea pig, and cat the corpus luteum may be removed comparatively early without harmful effects to the embryo or fetus. The rat occupies an intermediate position: early removal is followed by abortion, late removal is not in every case. In some species, e.g., the horse, the corpus luteum degenerates spontaneously; a type of gonadotrophic activity then follows, which is attributed to the placenta; and new corpora lutea are formed, which, however, do not persist throughout pregnancy. In a few other species also the corpus luteum does not persist, e.g., in the bat, *Nycteris luteola*. Another species in which endometrial structures may have an endocrine function is the Chinese hamster, but the evidence is purely morphological.

The corpus luteum of pregnancy is usually a little larger than that of the cycle, and the uterine reactions are more pronounced. The latter are found both in the pregnant and nonpregnant horn in monotocous females but are not fully maintained in the nonpregnant horn, indicating that local factors are important. In ovariectomized females the corpus luteum may be replaced by a mixture of estrogens and progesterone before implantation; afterwards progesterone is sufficient, the placental tissue apparently secreting enough estrogens if they are necessary at this time. Estrogens are excreted in large amounts throughout pregnancy, the amount rising to a peak shortly before parturition. They do not produce the usual psychic and vaginal reactions be-

cause their action is inhibited by progesterone. In the mouse the vaginal epithelium mucifies, suggesting the modified action found when small amounts of estrogen are present.

The number of young produced at a time is believed to be mainly a function of the anterior pituitary. This is logical, since F.S.H. promotes the maturation of graafian follicles, and since more eggs are shed, especially in young females, when this hormone is injected. Other factors, however, are at work since loss of eggs and fetal atrophy, especially the latter, are high among animals so treated. The number of young born averages higher than usual, but it is within the normal range for the species.

In normal females loss of eggs is frequent. It may occur in species with open capsules by failure to enter the oviduct. External migration across the body cavity is possible, but it is probably very rare. Another cause of loss of eggs is failure of fertilization, failure to implant, and death before they can be recognized macroscopically. In some species of *Elephantulus* many more eggs are shed than are implanted; a hundred or more eggs may be produced and one or two implanted. A similar situation, but less in degree, is found in the Virginia opossum, and it occurs, more or less, in all species. Among the armadillos the opposite condition is found: one egg is shed and fertilized, then it divides and produces several embryos (polyembryony). Fetal atrophy also causes losses in all species. The causes are not well understood and they may be varied. The action of inherited lethal factors is one; an inherited influence acting upon the mother is another which has been found in rabbits. In extreme cases uterine or, more probably, abdominal accommodation, or maternal nutrition, may be factors. Uterine accommodation in itself seems not to be a factor since, when one ovary is removed, the normal species number of eggs are shed from one ovary and develop in one horn of the uterus.

The time taken for ova to travel through the oviduct is remarkably constant, about 3 to 4 days, especially when the wide species differences in the length of the oviduct are considered. Transit is rapid through the first part of the tube, slow through the next portion, and again rapid until the uterus is reached. Generally the relation of sexual receptivity to ovulation is such that spermatozoa are awaiting the release of the egg and it is immediately fertilized. In Canidae, however, it has to await fertilization, since when it is shed the first polar body has not been extruded and it is not mature. The spacing of the fertilized eggs in the uterus is performed through irregular movements of the uterine muscle, and, in females with bicornuate uteri, ova

may travel internally down one horn, across the body of the uterus, and up the other horn.

The duration of pregnancy varies with the species; from 11 to 12 days in the Virginian opossum to 22 months in the Indian elephant. Strictly speaking, gestation is longer than 12 days in the opossum since the young are born in a very immature state and are immediately transferred to the pouch in which embryonic development continues. The shortest true pregnancy is the 16½ days of the hamster.

Parturition is preceded by the degeneration or loss of the function of the corpus luteum, and, in view of the relation of this body to the maintenance of pregnancy, this must be a major factor in determining the duration. However, in species in which the corpora lutea may be removed without terminating the pregnancy, the period of gestation is the normal length if this operation is performed. On the other hand, gestation may be prolonged by injecting progesterone, though if this is done for more than a very few days, death of the fetuses results. The general conclusion seems justified that pregnancy ends because the secretion of progesterone or its equivalent ceases. Why this occurs is not clear. The primary cause may be a failure in placentation resulting in a fall in estrogen output. In this connection it may be noted that the corpus luteum persists if embryos are removed during pregnancy without disturbing the placentae, which continue to live.

Species differences in the duration of gestation are related to a variety of factors. In general, the larger an animal, the longer its gestation; but there are many exceptions, for example, the guinea pig and dog each with a gestation of about 64 days may be contrasted. In seasonal breeders there is a tendency for the duration of gestation and the breeding season to be so related that birth occurs at the time of year in which food is most abundant. For example, the horse breeds in spring and the young are born in spring; the goat breeds in the fall and the young are born in the spring; the roe deer breeds in summer and the young are born in spring; and the fallow deer breeds in early winter and, again, the young are born in spring. Another factor relates to the habits of the species. Those with burrowing habits, or which live most of their lives in concealment, have shorter gestation periods and the young are born in a more immature state than species who live in the open and depend upon speed as a protection. Thus, burrowing rodents and bears, which hibernate during and after pregnancy, are examples of the first, and deer are examples of the second class.

Variation within species is also observed. Some of this is related to the

size of the litter; the larger the number, the shorter the gestation. In monotocous animals males are carried a little longer and are a little heavier at birth than females. Hereditary factors also influence the length of gestation; Holstein-Friesian cattle have a mean gestation period of 279 days, whereas the Brown Swiss period is 290 days, with other breeds between these extremes. In a few species the season of the year has an influence. This is most noticeable in horses, in which gestations terminating in winter average about 20 days shorter than those ending at any other time of the year. Maternal influence is shown in hybrids. Thus the mare has a gestation of 335 days while the period for the ass is 365 days. The mare carries a hybrid for 345 days, less than the mean between the species and nearer her own period, while the ass carries a hybrid for 355 days, more than the mean and nearer her own period.

Delayed implantation is an interesting phenomenon found in some species, particularly in the Mustelidae. The duration of gestation in many of these, e.g., the European badger and the American marten, is about 250 days. Fertilization takes place in July or August, the egg develops for a few days, then lies dormant in the blastocyst stage until January, when it is implanted. Development now proceeds normally and birth is in March. Actually, the embryo is growing for about 50 days. The dormant period can be reduced by at least 3 months by exposing the pregnant females to artificial light during the winter, a result which suggests that activation of the pituitary gland is involved, though the injection of prolactin delays implantation. Other species with delayed implantation are the armadillo, the roe deer, and probably the bears and seals. The roe deer is interesting as this species breeds outside the normal season for Cervidae in the temperate zone, yet the young are born, because of this modification, at the usual time for the family as a whole.

Delayed implantation is also found in Muridae if the females become pregnant while they are suckling a litter. Gestation in these species is usually 21 days, but under the circumstances just noted it may be prolonged to 30 or 40 days. The degree of prolongation is related to the number of young being suckled, and it is greater as this number increases. The larger rodents, house rats and cotton rats, may not show this phenomenon, or if they do it is to a lesser extent than the smaller rodents, such as the mice. Experimental work has shown that the injection of estrogens causes prompt implantation in the lactating mouse, so the delay is due to a relative shortage of a specific

hormone. In rabbits heavy lactation increases the amount of fetal atrophy and may terminate the pregnancy altogether. In some species, such as the cow and primates, estrous cycles tend to be suppressed during lactation. All these facts suggest a depression of endocrine function or a diversion of its activity. The question of pregnancy during lactation leads to that of the postparturient heat. In several groups, the Cricetidae and Muridae, and in seals, this frequently occurs. In the first two families mentioned this heat is usually of short duration, and the vaginal and uterine reactions are atypical because parturition has just occurred. The factors which determine whether a species has a postparturition heat or not are unknown; even within one genus, *Peromyscus*, some experience it while others do not.

FACTORS INFLUENCING THE LIFE OF SPERMATOZOA

If they are to live long, spermatozoa must be comparatively inert. This means that their life in the female tract is somewhat limited. The vagina is especially unfavorable as an environment, and, in general, spermatozoa only retain their motility in this region for about 6 to 12 hours; the uterus is a little less unfavorable and the oviducts still less; but spermatozoa do not retain their motility for much more than 24 hours in any of these regions. The cervix is the least harmful part of the female tract. In several species in which the duration of fertilizing power has been tested, spermatozoa retain the ability to fertilize for little more than 36 hours, and lose it before motility disappears. If the latter is low, the spermatozoa are no longer able to find the egg. Important consequences of this short life are that spermatozoa are unable to survive from one heat period to another and that artificial insemination outside the normal heat period is nearly always ineffective. Species with long heat periods suffer in fecundity if coitus occurs only early in the period, e.g., the horse, since too few spermatozoa survive until ovulation.

Certain bats, i.e., some of the vespertilionids living in temperate regions and hibernating during the winter, were very puzzling to the research worker for some time, but the problem they presented has now been solved to some extent. Copulations have been observed during the heat period, which occurs in the fall. The females then go out of heat, and ovulation occurs in the spring, several months later. The spermatozoa, meanwhile, embed themselves in the mucous coat of the uterus and emerge about the time of ovulation. The question arises whether these spermatozoa retain their fertility

or whether another copulation is necessary in spring, during the last few days of hibernation, for fertilization to occur. The problem has been solved by Wimsatt, who succeeded in keeping bats alive in a refrigerator through the winter and in proving that fertilization of the eggs did occur in spring from the uterine store of spermatozoa. However, the possibility has not been ruled out that another copulation does occur in spring in the wild even though it may be unnecessary. Observation is difficult at this time because of the migratory habits of the bats. The males are capable of spring inseminations although the seminiferous tubules are inactive at this time. Spermatogenesis occurs in August, and the spermatogenic tissue soon retrogresses, but the interstitial tissue remains active and maintains the accessory organs throughout the winter. A store of spermatozoa in the epididymides is maintained, and they are capable of motility in the spring. The interstitial tissue and the accessory organs retrogress after the bats emerge from hibernation.

The long life of spermatozoa in the epididymis of the bat is exceptional. In other species fertility is retained for about 40 days, while motility lasts a little longer. The generally greater length of life in the male tract as compared with sperm longevity in the female tract is partly the effect of immotility and partly of lowered temperature in the scrotum. If the epididymis is anchored in the body cavity, at a higher temperature, fertilizing power is lost in about 8 days; motility is retained for a few days longer, but the spermatozoa are incapable of swimming far enough to find the eggs.

A question that has been much debated is how the spermatozoa reach the egg. The presence of the flagellum suggests that they are capable of reaching the eggs of their own volition, but, in all species examined, the time taken to reach the infundibulum does not differ much in spite of the vast differences in the length of the female tract. In some species, e.g., the rat, spermatozoa are injected directly into the uterus; in others, e.g., the cow, apparently they are not. Rhythmic uterine contractions probably aid in sperm transport and the same mechanism operates in the oviducts. Except during parturition the uterine muscle is most active during heat. An average of 4 hours is needed for spermatozoa to reach the infundibulum in all species examined, and about one million spermatozoa are needed at an insemination to make sure of fertilization. The first few sperm to reach the egg do not fertilize it but supply an enzyme, hyaluronidase, which causes the granulosa cells of the cumulus oöphoron to disperse, as Rowlands and Pincus have shown.

THE MALE ACCESSORY ORGANS

The functions of the glandular accessory organs are practically unknown. It has been held that some secretion from them is discharged in advance of the wave of spermatozoa to cleanse the urethra of substances toxic to these organisms, and also that these secretions serve a nutritive function. They can be excised without greatly depressing fertility, and, since the vesiculae seminales are absent in Canidae, these organs cannot be of vital importance to the spermatozoa. Secretions from the accessory organs form the vaginal plug found after coitus in rodents and in some other species, because of the power to coagulate semen possessed by some ingredient. This plug is believed to be conducive to fertilization as it permits a gradual release of spermatozoa as it disintegrates. The chemistry of the reactions involved has not been adequately worked out, but there is evidence that coagulation depends upon the interaction of an enzyme, vesiculase, produced by the prostate gland or by a branch of the seminal vesicle upon a protein secreted by the seminal vesicles. The semen of dogs, which do not possess vesiculae seminales, does not normally clot, possibly because of this fact; but it has also been shown by Huggins and Vail that the prostatic fluid contains a substance that prevents the clotting of fibrinogen. Human semen clots and liquefies shortly afterwards. In man the prostatic secretion contains a fibrinolysin. The semen of some species with vesiculae seminales, e.g., the horse and bull, does not coagulate, so there must be species differences in the composition of the fluids secreted by the accessory organs. Our knowledge of the biochemistry of the constituents of semen is scanty, and much remains to be learned in this field. So far little is to be found in the literature except general analytical data and pH determinations for a very few species of domestic mammals. It is interesting to note that human semen is much more highly buffered than is that of any other species which has been examined (Willett and Salisbury). This fact may be related to the high acidity of the female reproductive tract, thus protecting the spermatozoa from its influence.

The epididymis is the storehouse of spermatozoa and so, to a lesser extent, is the enlarged ampulla of the vas deferens found in some species, e.g., in the bull, though motility in this region lasts only 72 hours. Young has shown that the fertilizing power of spermatozoa taken from the head of the epididymis is less than that of spermatozoa taken from the tail. It is believed,

therefore, that, as they travel through the epididymis, some essential maturation process takes place. The time taken for this passage is about 3 weeks.

Slijper has studied the structure of the penis in its relation to the duration of coitus. He has classified the types of penis as follows:

Indifferent type	Rodentia Edentata	Moderately brief coitus
Fibroelastic type	Selondontia (Ruminants) Cetacea	Very brief coitus
Vascular type	Perissodactyla (Carnivora) Primates (Chiroptera, Insectivora)	Moderately long or very long coitus
Intermediate type	Subungulata (Proboscidea, Sirenia) Neobunodontia (Suidae, Hippopotomidae)	Intermediate length of coitus

In many insectivores the vagina is S-shaped during the heat period, and the penis adapts itself to that shape.

The work on bats, in which spermatogenesis and activity of the interstitial tissue are not always synchronous, has helped to prove that the male hormone, testosterone, is the product of the latter. This dissociation of the two testicular functions is interesting and deserves further study from the point of view of the pituitary hormones involved, especially as work upon American and European species is not entirely in accord.

The question of an annual period of rut in males also needs more study. The males in some seasonal breeders, e.g., the Sciuridae, have a definite season in which the testes and accessory organs are active, corresponding with the season of the female. Others, e.g., the ram, produce spermatozoa all the year round, but in some breeds spermatogenesis is at a low ebb in summer. McKenzie has suggested that this condition is due to a partial failure of the thermoregulatory function of the scrotum. It appears to be more frequent in breeds with a coating of wool upon this part of the body.

In general, females are smaller than males. This is due to the effect of estrogens upon the epiphyses of the long bones. The injection of these hor-

mones causes the latter to ossify, thus causing growth to cease, as Gardiner has shown. Rats kept unbred remain smaller than their litter mates, since growth is resumed during pregnancy, probably because of the inhibition of estrogen by progesterone. Ovariectomized females, in which no estrogens are circulating, grow to a larger size than do normals. It would be interesting to compare the growth curves of pseudohermaphroditic goats with those of normal males and females, since the first are genetic females with a male hormonic constitution.

PART II

THE FABRIC

MONOTREMATA

ORNITHORHYNCHIDAE

Ornithorhynchus paradoxus Blumenbach

DUCK-BILLED PLATYPUS

THE female platypus begins to breed when she is 16 inches long, but whether this is during the first or second season is uncertain. The adult length is about 18 inches. She breeds once a year, in July or August to mid-October. The breeding season is early in Queensland (July–August) and later in Victoria (September–October). Early in the season the testes, the crural glands, and the scent glands of the males enlarge. Copulation occurs in the water (1).

Only the left ovary is functional (2), and the eggs are always found in the left uterus (1). These are round and are 3 mm. in diameter at the time of fertilization; they immediately grow by imbibition of water and become oval. The number shed is 1 to 3, usually 2. As they pass down the oviduct, they receive a coat of albumen and a thin, leathery shell (3). In the uterus the eggs are apart, with the longer axis in the direction of the length of the uterus. At laying, the female squats in the nest on her rump with her tail between her legs and hands to receive the eggs (1). As it is laid the egg measures 16 to 18 mm. $\times$ 14 to 15 mm. (3). When two are laid they soon join, side by side (1). The sticky material which causes them to cement together is deposited in the oviduct (3). The average number of eggs or of young found in nests was $1.9 \pm .04$ (1).

Ovulation is followed by the folding of the follicular wall, which reduces the size of the cavity. This becomes partially filled with extravasated blood. The theca externa grows in to form lobule walls, and theca interna cells increase in numbers to form syncytial masses. The granulosa cells hypertrophy and produce the lutein tissue. The fully formed corpus luteum is 4.5 mm. $\times$ 3.5 mm. in diameter. Retrogression begins shortly before the eggs are laid and is accompanied by the invasion of numerous leucocytes. The formation of the corpus luteum in this, the most primitive mammal, is typical of that of most species (4).

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ECHIDNIDAE

Echidna aculeata Shaw

In Tasmania the echidna breeds from near the end of June to the beginning of September (1). It breeds once a year and lays one egg, which is placed in the pouch by the mother. The pouch is visible in the embryo, but after hatching it is lost to sight until the beginning of the first heat (2). Normally one egg is produced, although there were 4 exceptions in 140 cases. Both ovaries are functional, contrary to earlier statements. The passage through the oviduct is rapid. The first polar body is given off in the ovary and the second in the oviduct. With its coating of albumen and shell the egg is 4 mm. in diameter (1).

The oviduct consists of an infundibulum, a neck, and an albumen-secreting layer. The infundibulum is lined with tall, columnar, nonciliated secretory cells and with ciliated nonsecretory cells. The fluid from the secretory cells is clear and is secreted prior to ovulation. It is very plentiful and fills the space between the ovary and the infundibular membrane. The neck contains gobletlike mucoid cells, which secrete just before the egg leaves the follicle and early in fertilization. This secretion is not plentiful. The albumen-secreting cells produce two layers which cover the egg. The first layer is dense and is deposited during passage through the upper two thirds of the tube. It is produced mainly during the fertilization stages. The lower third produces the second layer of albumen, which is more fluid and is small in amount. This part of the oviduct is glandular, containing convolated tubular glands as well as the secretory epithelium. The glands secrete before the ovum leaves the follicle, and the fluid is stored in the lumen (3).

At the tubo-uterine junction are more glands, which, with the glands of the tube, deposit the two-layered shell. The shell material is secreted by the basal part of the glands, while their middle and upper regions secrete a kind of uterine milk (3).

The intra-uterine period of incubation of the egg is said to be about 28 days (4), but the evidence only justifies the conclusion that it is between 12 and 28 days.

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MARSUPIALIA

TOO little is known of reproduction in the marsupials to make any definite statements, but the pattern is not uniform. In general, the behavior of families of these animals appears to resemble that found in the corresponding Orders of Eutheria, an interesting extension to the physiological sphere of the anatomical adaptations which have arisen in the Order.

Most, if not all, species have a fairly restricted breeding season. The chief peculiarity found in the Order is the well-known one that the young are born in a very immature state after a short gestation. Development is continued in the pouch, the growth of which is mainly under the influence of estrogens and, to a lesser extent, of progesterone. More work is needed upon this problem.

Polyprotodontia

DIDELPHIDAE

Didelphis azarae Tomes

The cycle of this marsupial lasts for about 7 days. The heat period, in the absence of the male, is not followed by a corpus luteum but by follicular atresia. The diestrous vaginal smear contains mainly leucocytes, which are not altogether absent at any time, but at the time of heat cornification of the wall sets in (1).

1. Martinez-Esterre, P. Compt. Rend. Soc. Biol., Paris, 124: 502–504, 1937.

Didelphis virginiana Kerr

VIRGINIAN OPOSSUM

In Texas the breeding season of the Virginian opossum begins in January and lasts to October, with an anestrous period in November and December. The females are polyestrous and have at least two litters a year (1). The cycles recur at about 28 days, and heat lasts 1 to 2 days (2). Ovulation is spontaneous (3) and probably occurs early in heat (2). The ova pass through the oviducts in 24 hours or a little less. The average number of eggs shed is 22, and on removal of one ovary the remaining one sheds a larger number of eggs (3). The average number of young born is 10, range 8 to 12 (4). The duration of gestation is 12½ days and the young are born very immature (3).

HISTOLOGY OF THE FEMALE TRACT

OVARIES. During anestrum the ovaries are very small and are packed with follicles, mostly in a state of atresia. No corpora lutea are present at this time. The corpus luteum reaches full size by 3 days after ovulation. It is maintained for 7 to 8 days, then it becomes a dirty yellow because of its lessened vascularity, and by 20 days it has almost disappeared (2). Six per cent of opossums have accessory ovarian tissue as stalked outgrowths from the ovaries (5). The ovaries are unique in the frequency of polynuclear ova, found in 93 per cent, and of polyovular follicles, found in 60 per cent of the ovaries studied (6).

VAGINA. The vulva is within the rim of the cloacal aperture. There are a blind median vaginal canal and lateral ones shaped like interrogation marks. Spermatozoa travel up the lateral canals, and birth is by a temporary connection between the uterus and the median canal (3). The latter is lined during anestrum with an epithelium, 5 to 6 cells deep, of low columnar cells becoming flat next the lumen. At proestrum this grows to 12 to 15 cells deep. Mitoses are abundant and no leucocytes are present. The vaginal smear consists mainly of large nucleated cells. At heat cornification sets in, with massive desquamation late in the period. There are no epithelial cells or leucocytes in the estrous smear, only cornified cells. During metestrum leucocytes invade the

epithelium and appear in the smear. By 4 to 5 days epithelial cells have reappeared, and the smear also contains an occasional leucocyte as well as vacuolated epithelial cells. The lateral canals do not open until puberty. Sloughing in these organs is a more continuous process than it is in the median canal and is not limited to the end of heat. Cornification begins a little earlier; few leucocytes appear and most of the removal of debris is done by bacterial decomposition (2). During heat these canals are greatly distended by clear, thin, stringy mucus; just after heat they retrogress and are filled with a dry, cheesy mass of cell debris (3).

UTERUS. During proestrum the uteri are large, vascular, and turgid. After ovulation they swell and reach their maximum size at 5 to 6 days, while they are reduced by 13 to 15 days. In anestrum the glands are straight or slightly coiled, and the uterine epithelium is low columnar or cuboidal. During heat the endometrium is more vascular and is edematous. Mitoses are present in the epithelium, which tends to become pseudostratified. The glands contain ciliated epithelium. In heat the glands are greatly coiled, their lumens are enlarged, and the epithelium is actively growing and is pseudostratified. During the lutein phase conditions are much the same, but there are fewer mitoses in the glands and the epithelial nuclei are basal. In later stages the capillaries are exceptionally large. At 15 days the endometrium is invaded by leucocytes, and by 20 days the uterus has returned to the resting stage (2).

The tubo-uterine junction has no folds of mucous membrane but is protected by a sphincter. The last 3 to 4 cm. of the tube contain numerous glands, and the lumen is much wider than it is in the Eutheria. This portion is extremely tortuous, and it enters the uterus at the side, opposite the mesentery (7).

PHYSIOLOGY OF THE FEMALE TRACT

Ovariectomy is always followed by the death of the embryos because of the collapse of the central layer of the endometrium (8).

The ovaries may be stimulated to secrete estrogens by the injection of P.M.S., if this is done from 100 days of age onward. Before this age the response given is the precocious conversion of embryonic egg nests to primordial follicles (9).

THE MALE

Spermatozoa are present in the testes of males at all times of the year (1). The testes increase in size from the age of 16 days to 60 days, then more slowly from 83 days to maturity. The seminiferous tubules are quiescent to day 100. Spermatozoa are present by 8 months, and androgens are secreted by 5 months (10).

Castration at 22 days of age is followed by typical prostate differentiation (11), and the same is true for Cowper's glands and Bartholin's glands, at least for the first hundred days (12), but sex hormones do stimulate growth and histological differentiation (13). Young males treated with P.M.S. secrete androgens by the seventieth day of life or a little earlier (9).

As the young are born in a very immature condition, they afford a good opportunity to test the action of androgens and estrogens during what, in other species, is embryonic and fetal life. Androgens only mildly stimulate the Wolffian ducts in males, but in females the effect is greater and the ducts are preserved in an atypical manner. The effect on the Mullerian ducts is slight in the male, but extreme stimulation results in the female. Cessation of treatment is not readily followed by involution. The development of the prostate in males is markedly hastened and it is stimulated in the female, but there is little effect upon the testes and ovaries. Phallic stimulation is marked in both sexes, and the clitoris becomes a typical penis with a bifurcate glans (14).

Estrogens are decidedly toxic. The Wolffian ducts are stimulated in both sexes, more so in the male than in the female. There is localized stimulation of the Mullerian duct in the male. In the female it is precociously stimulated, with glandular development. Tremendous hyperplasia of the urogenital sinus occurs in both sexes with metaplasia and sloughing of cornified cells. There is no appreciable effect upon the testes or ovaries. Prostate development does not occur in males, but previously formed prostatic outgrowths grow to enormous proportions (14).

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Other DIDELPHIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Chironectes minimus Zimmermann		Dec.–Jan. (Cabrera and Yepes)		S. America
C. panamensis Goldman Water Opossum				Cent. America. A pouch is present in the male (Enders)
Didelphis aurita Wied	Two seasons: June–July, end Oct. (Hill)		9	S. America. One record
D. marsupialis L.			2–7	Cent. America (Enders)
Marmosa isthmica Goldman	Breeds once a year, late Feb. or March (Enders)			Cent. America
M. murina L.			10	Cent. America. One record of pouch young (Enders)

Other DIDELPHIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Metachirops opossum L.	Apr.–July (Enders)		2–8	
Metachirus nudicaudatus Geoffroy Brown Opossum			1–3	Cent. America (Enders)

DASYURIDAE

Chaetocercus (*Amperta*) *cristicauda* Krefft

POUCHED MOUSE

Krefft's pouched mouse breeds from June to September, and seven young are usually born at a time. The female has practically no pouch; the young cling to her nipples for considerably over a month, and she staggers round with this burden (1).

1. Wood-Jones, F. The Mammals of South Australia. Adelaide, 1923–24.

Dasyurus viverrinus Shaw

MARSUPIAL CAT

The marsupial cat is monestrous and has one season a year, from late May or early June to early August, but the male does not appear to have a corresponding rutting season. Procestrum lasts 4 to 12 days and heat 1 to 2 days. Ovulation is spontaneous, and it occurs about 5 days after copulation or heat. The duration of pregnancy is therefore rather difficult to determine,

but it probably lasts 8 to 14 days. In its absence pseudopregnancy ensues (1). The number of eggs shed varies from 20 to 35 with 20 to 25 as the usual number (2). The number of embryos is correspondingly high, and as the number of nipples in the pouch is usually six a considerable wastage of embryos results (1). The young remain attached in the pouch for 7 to 8 weeks (3). The diameter of the egg averages 0.24 mm. (2).

The ripe graafian follicles are borne on projecting bosses, and when they rupture they decrease in size. There is but little intrafollicular hemorrhage. The corpora lutea grow in 3 days, are yellowish white, and persist for the greater part of lactation, about 7 to 8 weeks, after which they decline (3). It is practically impossible to distinguish two thecal layers, the whole structure resembling theca externa. There are no mitoses in the developing corpus luteum, and the theca produces connective tissue only (4).

Proestrum is marked by an edematous swelling of the lips of the cloacal aperture, and the pouch enlarges somewhat and becomes tumid as the result of the enlargement of the sebaceous glands in this area. The sweat glands enlarge and coil, causing the interior of the pouch to become moist and somewhat sticky. The uteri enlarge, vascularity increases, and the glands are coiled in the basal portions of the endometrium. The uterine epithelium is low columnar and is in a state of active mitosis. Leucocytes are abundant (1).

The changes during heat are a continuation of those observed in proestrum. The glandular epithelium is ciliated throughout. In the postestrous period, between heat and ovulation, the uterine condition is maintained, but the cloacal swelling gradually subsides. The first polar body is extruded while the egg is still in the ovary (1).

In pseudopregnancy the pouch continues to enlarge, and the development of the sweat and sebaceous glands reaches the level observed during pregnancy. Toward the end of the period the female often cleans out the pouch in the manner of the pregnant animal, as a preparation for the reception of the young. The uterine glands become very contorted and enlarged, so that the condition resembles the extreme lutein reaction observed in rabbits during pseudopregnancy. The epithelium is tall columnar. At the end of the period much cellular desquamation into the gland ducts occurs, and the uterine epithelium undergoes the same change. Leucocytes are abundant but there is no extravasation of blood. The duration of pseudopregnancy is probably about two weeks (1).

Copulation is very prolonged, up to about two hours, and spermatozoa

remain alive in the oviducts for about 2 weeks, an unusually long time which is probably related to the delayed ovulation in this species (1).

1. Hill, J. P., and C. H. O'Donoghue. Quart. J. Micros. Sci., 59: 133–174, 1913.
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3. Sanders, F. P. Proc. Linn. Soc., New South Wales, 28: 364–405, 1903.
4. O'Donoghue, C. H. Anat. Anz., 41: 353–368, 1912.

Other DASYURIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Antechinomys laniger Gould Jerboa Pouched Mouse		6–8		
Dasyurus geoffroyi Gould Marsupial Cat		6		
Myrmecobius fasciatus Waterhouse Banded Anteater	June–July (Jones)	4		No pouch
Sarcophilus ursinus Harris Tasmanian Devil		4	31 days	
Sminthopsis crassicaudata Gould Fat-tailed Pouched Mouse	June–July (Jones)			

PERAMELIDAE

Perameles nastuta Geoffroy

BANDICOOT

The bandicoot has no vesiculae seminales and no ampulla to the vas deferens. Spermatozoa can be found in the urine (1).

1. Bolliger, A., and A. L. Carrodus. Med. J. Australia, 25: 1118–1119, 1938.

Other PERAMELIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	HABITAT, ETC.
Choeropus castanotis Gray Pig-footed Bandicoot	June (Jones)	2	
Perameles eremiana Spencer Desert Bandicoot		2	
P. myosura Wagner Barred Bandicoot	May–June (Jones)	2–3, usually 2	
Isoodon obesulus Shaw Short-nosed Bandicoot	June (Jones)	4	
Thalacomys leucurus Thomas White-tailed Bilby	March–May (Jones)	1–2	In central area of S. Australia rain and food supply regulate breeding

Diprotodontia

PHALANGERIDAE

Trichosurus vulpecula Kerr

AUSTRALIAN OPOSSUM

The Australian opossum has two breeding seasons a year, in March and August. Birth occurs 16 days after mating, and the young remain in the pouch for 5 months (1). The age of puberty is 1 year, and the number of young is one. The breeding season is said to be June in South Australia with possibly two seasons in some areas. The young leave the pouch in Septem-

ber (2). In fully grown nullipara the pouch develops in January and February (3).

The male has no seminal vesicles or ampulla to the vas deferens, and spermatozoa may be found in the urine (4).

One injection of 900 I.U. of estrone into the immature female caused the characteristic yellowish-brown discoloration of the pouch area. The latter is increased in size. In the nonbreeding adult 900 I.U. had no effect, but 12,000 I.U. caused pigment development (3). The injection of 5,000 to 50,000 I.U. of estrogen into mature females caused the pouch to thicken and pigment to be secreted. The median vagina swelled, and its epithelium was keratinized. In parous females 200 I.U. of estrogen caused the pouch pigment to develop (1).

In pouch young, 3 months old, the injection of 2 mg. of progesterone once a week caused the pouch rudimenta to increase in size and orange-brown pigment to be secreted, but retrogression set in after 3 months in spite of continued injections. Complete pouch formation did not result as it did if estrogens were injected. In nulliparous females the injection of 2 to 5 mg. of progesterone weekly caused the pouch to retrogress to such an extent that it practically disappeared. Similar injections of 5 mg. of progesterone weekly into a multiparous opossum with a large pouch caused it to retrogress in 3 weeks (5). The injection of progesterone into immature males caused the testes to ascend (6).

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Other PHALANGERIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	HABITAT, ETC.
Dromica concinna Gould Elegant Dormouse Opossum	Probably polyestrous, pouch young found Jan., July, Sept. (Jones)	1–6, av. 5	

Other PHALANGERIDAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	HABITAT, ETC.
Phascolarctos cinereus Goldfuss Koala Bear	Monestrous annually, end Oct. Males rut at same time (Semon)	1	
Pseudochirus cooki Ogilby Tasmanian Ring-tailed Opossum		1–6, usually 3	
P. longinosus Gould Ring-tailed Opossum	Early in year. Monestrous (Jones)	2	Young leave pouch end of April

MACROPODIDAE

Bettongia cuniculus Ogilby

RAT KANGAROO

The rat kangaroo in Tasmania breeds at least from March to December, probably all the year, and is polyestrous. Ovulation is spontaneous, and one ovum is shed at a time. There is a postparturition heat. Pregnancy is normally in alternate uteri, and while one is pregnant the other remains in a pseudopregnant state for the whole period. Lymph is expelled from this uterus just before parturition. The period of gestation is probably 6 weeks. Puberty is early, when the young are reasonably free from the pouch (1).

During heat mitoses are frequent in the endometrium, the epithelial cells show vacuolar degeneration, the gland cells are actively dividing, and the stroma is very edematous and is invaded by polymorphs. The epithelium and glands are strongly ciliated. In early pseudopregnancy (or pregnancy) there are no mitoses and fewer cilia and the glands are convoluted and actively secreting. Later, the epithelium is low columnar, cilia are few, the number

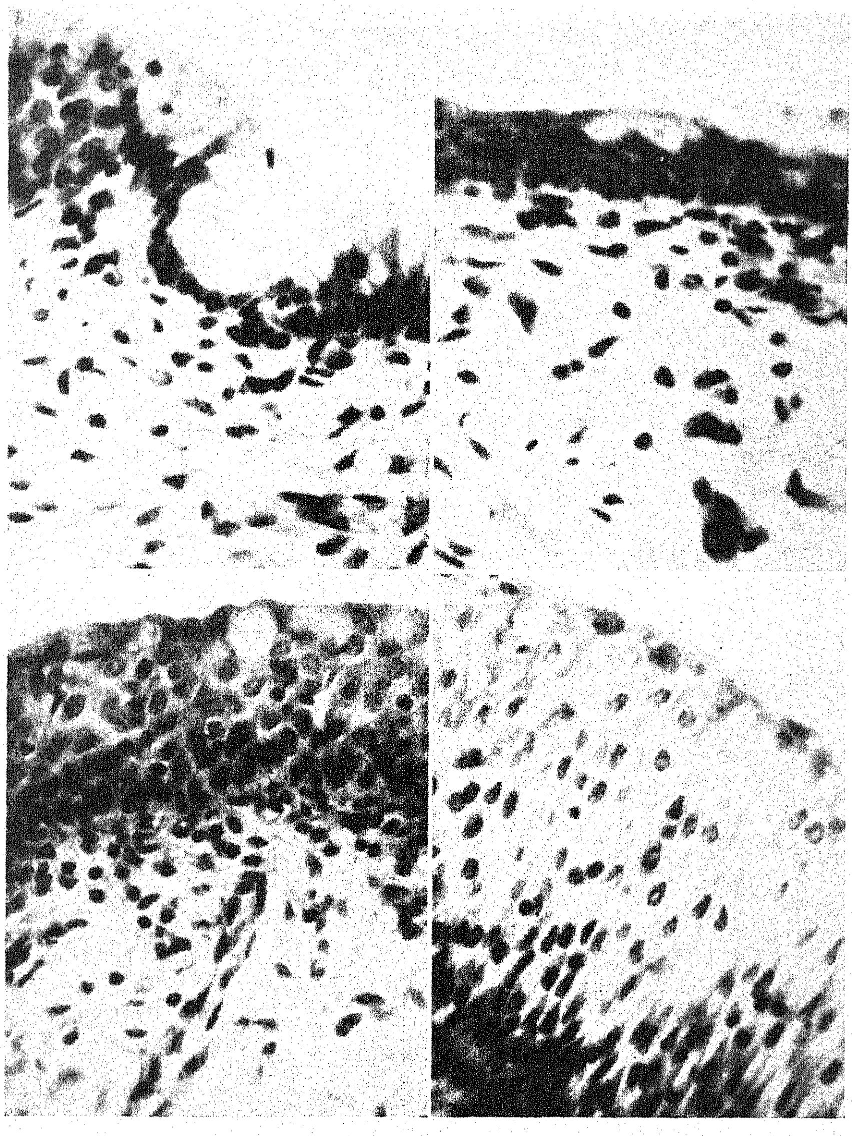

PLATE III. Vagina of cow, mucifying type of change in cycle. *Upper left:* Section near cervix, two days postestrum. Note height of the mucous cells. H and E. x400. *Upper right:* Section near cervix, twelve days postestrum. Note collapsed state of mucous cells. H and E. x400. *Lower left:* Section near vestibule, two days postestrum. Note mucous cells in outer layer of epithelium. H and E. x400. *Lower right:* Section near vestibule, twelve days postestrum. Note flattened mucous cells and growth of epithelium. H and E. x400.

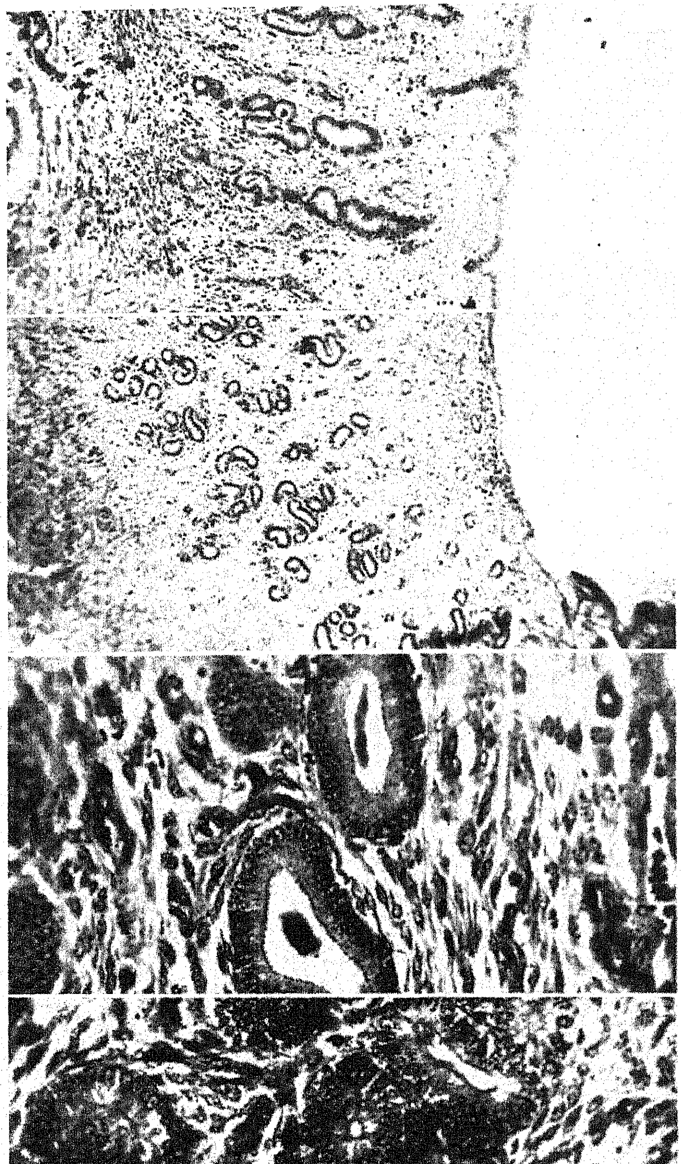

PLATE IV. Uterus of guinea pig, changes in cycle. *First:* In heat. H and E. x61. *Second:* Ten days postestrum. Note growth and coiling of glands. H and E. x61. *Third:* In heat. H and E. x300. *Fourth:* Three days postestrum. Note glandular cells full of secretion. H and E. x300.

of capillaries increases greatly, and the glands straighten near the surface and remain convoluted near their bases. Then the epithelium disintegrates, a great invasion of leucocytes occurs, and connective tissue cells move up and replace the surface epithelium (1).

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Caloprymnus campestris Gould

RAT KANGAROO

The male has no vesiculae seminales or ampulla to the vas deferens. Spermatozoa are found in the urine (1).

1. Bolliger, A., and A. L. Carrodus. Med. J. Australia, 25: 1118–1119, 1938.

Other MACROPODIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Bettongia lesueuri Quoy and Gainard		July	1		Leaves pouch in Nov., after a pouch life of nearly 4 months (Jones)
Hypsiprymnodon moschatus Ramsay Australian Muskrat			2		
Macropus fuliginosus Desmarest Sooty Kangaroo	Once a year (Jones)	Jan., remains in pouch until Oct.	1		
M. giganteus Zimmermann	Once a year (Jones)		1	38–40 days	

Other MACROPODIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
M. ruficollis Desmarest Wallaby	Aug.–Sept. and Dec.–Jan. (Hill)			40 days	
M. rufus Desmarest Red Kangaroo	Once a year (Jones)		1	30–40 days	
M. (Thylogale) eugenii Desmarest Scrub Wallaby	Once a year (Jones)		1		
Petrogale pearsoni Thomas Pearson Island Rock Wallaby		Leaves pouch Nov.–Dec. (Jones)			
Potorous tridactylus Kerr			1	Probably 6 weeks	

INSECTIVORA

THE insectivores need much more investigation, especially as the little that is known reveals some interesting patterns. This is particularly so in the families whose position is somewhat uncertain: those which are placed by some in this Order and by others in the Primates. In certain species of *Elephantulus,* for instance, much larger numbers of eggs are shed than embryos develop, the condition resembling that found in some marsupials, while the bleeding from the uterus, probably at the end of diestrum, may bear some relationship to the primate menstruation. Induced ovulation is probably rather frequent in some families, e.g., in the Soricidae. Another interesting point is that the corpus luteum of pregnancy does not seem to be of much importance in the maintenance of gestation. The interstitial gland in female European moles, with its growth parallel to that of the clitoris in the nonbreeding season, deserves further study. Its embryology and the possibility of its occurrence in other Talpidae are worth investigating. Altogether this Order appears to offer a more fertile field for study than any other.

MACROSCELIDIDAE

Elephantulus myurus Thomas and Schwann

The classification of the South African elephant shrews has presented some difficulties to the systematists. Allen (1) gives two subspecies of *Elephantulus rupestris* A. Smith, namely, *jamesoni* and *myuri.* Van der Horst gives the names of the subspecies with which he works as *E. myurus jamesoni.* He states that *E. rupestris* sheds only 2 eggs at a time (2), while *E. myurus jamesoni* sheds about 120, so the classification used by him is probably more nearly correct.

Other MACROPODIDAE (*Continued*)

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These shrews have been found pregnant in September in South-West Africa and in April and May in East Africa. The number of young is 1 to 2. The testes are internal; the penis is abdominal, long, very slender, and vermiform (3). The species is apparently seasonally polyestrous (4). Up to 60 ova are shed from each ovary, but only one is found in each horn. The eggs pass rapidly through the first part of the oviduct and collect within a swelling of the central part of this tube, remaining there for some time, after which they pass rapidly through the remainder of the tube. The central portion of the oviduct, termed the egg chamber, is nonciliated. Transport through the last part is by means of weak muscular contractions (5). The embryos remain at the 4-cell stage until they are implanted (6). Bleeding and desquamation occurs from a polyplike growth in the uterus apparently at the end of diestrum (4).

THE FEMALE TRACT

OVARY. The amount of fluid in the graafian follicles diminishes before ovulation until it remains as a narrow rim between the cumulus oöphoron and the granulosa. The latter layer enlarges and its cells begin to luteinize before ovulation (7,8). The theca cells enlarge and multiply, but only in the deeper part of the follicle. As ovulation approaches, the granulosa cells at the cap of the follicle move toward the interior. At ovulation this attenuated cap tears off, and the contents of the follicle bulge out and spread over the surface of the ovary, so that the contents of the numerous everted follicles tend to fuse. The theca grows outwards as a core to each corpus luteum, and the whole structure becomes more convex, giving the peripheral layer a compact appearance. Germinal epithelium grows over the lutein masses. Gradually the thecal cores diminish in amount, leaving a layer of granulosa-lutein cells covered by one of germinal epithelium. These changes have not been accurately timed, but the last stage is reached before the uterine polyp is formed. The lutein tissue is fully encapsulated during the polyp stage, and the corpus luteum is degenerating when it begins to show necrotic changes (see below). The mode of vascularization of the lutein cells is believed to differ from that found in other mammals as groups of 4 or more cells are arranged in close relation to a capillary loop in contrast to the usual investiture of each cell with a capillary network of its own (8).

UTERUS. In the immature elephant shrew the uterine epithelium con-

sists of low columnar to cuboidal cells with compressed nuclei arranged so that the epithelium has a pseudostratified appearance. The stroma has a narrow subepithelial cellular zone 15 to 20 μ thick, and the cells are basophilic. The glands are shallow. In anestrum the appearance is the same except that secretion is found in the lumen of the uterus and the glands appear to be cystic (4).

The estrogenic phase at the beginning of the breeding season is marked by great edema of the endometrium, particularly in its basal portion. The glands increase in length, but remain straight; the cells divide and enlarge. As heat progresses, the edema spreads toward the lumen of the uterus, and the stromal cells become vacuolated; late in heat polymorphs invade the endometrium. At ovulation red blood cells are extravasated in the region of the thickened stroma, i.e., in the superficial layer (4).

During the lutein phase the edema slowly subsides, earliest from the superficial layers in which it has appeared last. The epithelium is high columnar and pseudostratified; the glands become coiled. When the corpus luteum begins to degenerate, the uterine muscle contracts, and a polyplike body develops as part of the endometrium projecting into the lumen from its mesometrial pole. It is accompanied by considerable local edema, and the glands dilate. The epithelial cells become exceedingly tall, and the polymorphs which had previously invaded the endometrium disappear. Eventually the growth forms a pendulous mass hanging down into the uterus (4). This structure does not develop if pregnancy and implantation occur so that it is essentially a part of the cyclical changes (9).

At a time which is evidently the end of diestrum, the capillaries in the polyp dilate and lacunae appear in the subepithelial layer. Bleeding occurs into the glands, cellular necrosis sets in, and the structure enlarges because of the edema and bleeding. Then the epithelium ruptures, and the whole necrotic mass pours out into the lumen of the uterus. Regeneration is rapid and it may overlap the estrogenic phase, so that late in the season the uterus of the shrew in heat may present a very complex series of changes. The writers cited believe that this very remarkable series of changes may be a forerunner of the menstrual changes found in the higher primates, and, in view of the disputed systematic position of this genus, the suggestion is interesting (4). Another interesting point is the partial resemblance between the formation and coalescence of the corpora lutea in this species and the way in which among New World monkeys they coalesce with the interstitial tissue by the disappearance of the thecal coat.

If coitus occurs and the female is fertilized, most of the ova begin their development, but, as the area of possible implantation is limited, only one is implanted and develops. The remainder are mostly imprisoned in the upper part of the uterus by a strong contraction of the circular muscle and degenerate at the 1-, 2-, or 4-cell stage (10).

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Other MACROSCELIDIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Elephantulus capensis Roberts			2	S. Africa. About 120 eggs released (van der Horst)
E. intufi A. Smith Elephant Shrew	Pregnant Nov., March		2	S. Africa. Two eggs shed (van der Horst)
E. rozeti Duvernoy				N. Africa. Pectoral glands develop with testes (Long)
Macroscelides proboscideus Shaw	Pregnant Aug., Sept.		2	S. Africa. Numerous eggs released (van der Horst)
Nasilio brachyrhynchus A. Smith	Pregnant June, Nov.	April	1–2	Cent. Africa
Petrodromus tetradactylus Peters	Pregnant Dec.		1	Cent. and S. Africa. One or two eggs released (van der Horst)

CHRYSOCHLORIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Chrysochloris damarensis Ogilby Golden Mole	April–July (Broom)	July–Aug.	2	S.W. Africa

ERINACEIDAE

Erinaceus europaeus L.

EUROPEAN HEDGEHOG

The hedgehog is said to be monestrous with two seasons a year (1), and litters are born in May–June and August–September (2). Ovulation is spontaneous, and the usual litter size is 5 (3). The gestation period seems to be variable as two reports give 34 to 49 days (4) and 35 to 40 days (5), respectively. However, it is difficult to obtain accurate data as captivity is detrimental to reproduction in this species. The earlier-born young do not reach puberty in their first year (3).

The ovaries are roughly U-shaped, bent round a thick muscular hilus, and are exceptionally well vascularized. They are completely enclosed in a tough capsule, and the stroma is fibrous with some fat-containing cells. Pigment is very common in both the ovaries and uterus, especially during the breeding seasons. During the winter anestrum immature ova only are found and follicular degeneration is especially marked. Besides the usual types of atresia, another occurs in which several small follicles collapse producing glandular-looking cell masses. In April the ovaries become active (3).

There is a remarkable growth of the granulosa during the period of follicular expansion, and the preovulatory size of the follicle is 1.25 mm. In the absence of mating these cells fail to luteinize although normal vascularization occurs; blood is extravasated and fibrous tissue grows. The fully formed corpus luteum of ovulation is 0.7 to 1.0 mm. in diameter; it contracts to

0.5 mm. at the next ovulation and remains stationary at that size for some time, but the corpora remain separate, seldom becoming confluent as do those of pregnancy and of pseudopregnancy. After copulation pseudopregnancy is frequent, and the corpus luteum then formed is the usual type, with luteinization of the granulosa cells. This type grows to 1.1–1.4 mm. The corpus luteum of pregnancy is similar to that of pseudopregnancy. New follicles grow and reach the size usual at estrus, but they degenerate. The corpora of pregnancy and of pseudopregnancy often become confluent, and they are very slow to retrogress. After copulation the general vascular condition shows a marked increase. The ovum is 70 μ in diameter (3). There is no postparturient heat.

The vagina is large and muscular; it remains open at all times. In the upper part the lumen is large and the wall relatively thin; in the middle region it is more muscular, the lumen is much smaller, and a pair of large glands are present.

The lower vagina is still narrower, with large lymph nodes and numerous accessory glands embedded in the wall. The vagina is greatly dilated during heat; it does not subside during diestrum but does in pseudopregnant cycles. The inference may be drawn that the hedgehog is not truly monestrous, but only appears to be so in the wild state. The epithelial cycle is normal, with growth, cornification, and sloughing, which is most marked in the upper vagina. The vaginal glands regress during anestrum (3). There is considerable secretion of mucus by the glands during the breeding season (1).

The horns of the uterus are short, thick, and muscular and at their junction lie almost at right angles to the cervix and vagina. Well-defined cervical fornices are present. No striking changes occur in heat or in the noncopulatory cycle, but in proestrum new glands develop from epithelial ingrowths. In pseudopregnancy the epithelium is much folded, there is slight growth and secretion, and the stroma becomes edematous. In pregnancy one finds some early epithelial destruction and extravasation of blood and pigment into the lumen (3).

The oviduct is bent round so that it lies against the tip of the uterine cornu. There is a conspicuous parovarium. The ciliated epithelial cells grow as estrus approaches, and after ovulation some cells slough off and secretion is apparent, but none of the changes are marked. The tube becomes edematous during the breeding season (3).

During the winter anestrum follicles will ripen and the reproductive tract

enters the estrous condition if females are kept in the laboratory at a temperature of 70 to 75° F. The temperature seems to be more important than increasing the daily amount of light. However, ovulation rarely occurs among these animals (6).

The male has a definite breeding season with spermatozoa from April to August. There is no true scrotum but the testes descend into a perineal pouch. The accessory organs are very large during the breeding season. In September or October the whole tract rapidly becomes smaller and, after a period of dormancy, again increases in March of the following year. The seminal vesicles increase sixtyfold in weight from anestrum to rut. In the sexually active animal the reproductive tract may represent 10 per cent of the body weight (2,7). The interstitial cells of the testis proliferate during the spring and begin to retrogress toward the end of July. In fall and winter this tissue is atrophic. The accessory organs parallel the interstitial cell development, and their involution is rapid after castration (8). Although spermatozoa are not produced during the nonbreeding season, some spermatocytes are always present, but the male does not respond to the stimulation of laboratory conditions as does the female (7).

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Other ERINACEIDAE

SPECIES	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Aethechinus frontalis A. Smith South African Hedgehog	Summer	2–7, usually 2–4	
Atelerix pruneri Wagner		4	N. Cent. Africa. One record

TENRECIDAE

Tenrec ecaudatus Schreber

TENREC

The tenrec of Madagascar might be an interesting animal to investigate as seven embyro counts range from 16 to 32, with an average of 21 (1,2).

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TALPIDAE

Condylura cristata L.

STAR-NOSED MOLE

The star-nosed mole of eastern North America is said to mate in November and to have two or more litters a season (1). The latter is not certain as the young appear to be born in a limited season, extending from mid-April to mid-June, with most born about the end of the first week in May (2). The average number of embryos is $5.8 \pm .2$ with a range of 4 to 7, and a mode of 6.

The testes and bulbo-urethral glands enlarge late in January (2), which indicates that the record of mating in November may be in error.

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2. Hamilton, W. J., Jr. J. Mammalogy, 12: 345–355, 1931.

Parascalopus breweri Bachman

HAIRY-TAILED MOLE

The hairy-tailed mole of eastern North America mates from the end of March to the first week of April and has one litter a year. The litter size is

usually 4, and the gestation period between 4 and 6 weeks. The vaginal orifice is closed except during the reproductive season; it is open before mating and is closed by September. The testes are enlarged early in March, decrease rapidly to June, and then gradually subside to their minimum size in September and October (1). These moles are sexually mature in the spring following their birth (2).

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Talpa europaea L.

COMMON EUROPEAN MOLE

In Great Britain the common European mole breeds once a year, in spring or early summer (1), according to one report, but another gives the main season as lasting from the end of March, usually April, to early May. Occasionally later litters are born in August or September (2). In Russia the season is said to begin in mid-April and to extend into August, though most young are born at the end of May (3). The average litter size is 3.76 ± .07, with a standard deviation of 0.84 and a mode of 4. The range is 1 to 6 (2). The vagina is closed except in the breeding season. Before it opens the surrounding area becomes purplish blue and congested; when it is open this area swells. These changes commence in Great Britain in the first half of March and are complete by the end of the month. The vagina begins to close immediately after parturition. The vaginal canal is a solid epithelial strand, 5 cells thick, which increases to 6 to 15 cells as those at the center become stratified and desquamate to form the lumen. It closes by constriction of the surrounding muscle fibers. There is no os uteri, and the cornua open into a median uterovaginal canal which is open for about 15 mm. and closed for the caudal 5 mm. As this canal grows in proestrum, it doubles in length and assumes a sigmoid curve. It diminishes in length as soon as the animal becomes pregnant (1).

The oviducts lie mostly in the wall of the ovarian capsule. The uterine cornua increase in length during the breeding season, and, during heat, the blood vessels in the endometrium greatly develop, especially on the mesometrial side, and on this side, also, the circular muscle hypertrophies (1).

The ovaries are remarkable bodies. A type of tissue resembling interstitial tissue is massed separately from the true ovary. The capsule forms the outer layer of the interstitial part and pouches the ovigenous part, which is covered by germinal epithelium. There is also some interstitial tissue in the true ovary. Furthermore, in the uteri of a minority of moles, believed to be old ones, masses of tissue resembling interstitial cells are found. The ovarian interstitial gland has a definite cycle, which is opposite to that of the rest of the reproductive tract. It is least in size during heat and in pregnancy, which lasts about 4 weeks. The clitoris is peniform and grows or diminishes with the interstitial tissue. The corpus luteum persists throughout pregnancy but disappears quickly during lactation (1).

The testes begin their development in January. By the end of March spermatozoa are present, but spermatogenesis begins to lessen at the end of April, and there is not much further activity until the following January. The interstitial tissue of the testis is large and is bathed in plasma from March to mid-April. At the end of this time these cells begin to be laden with yellowish-brown pigment. In May the plasma has disappeared, and there is little further change until the following January, except that the pigment does not appear to persist throughout the nonbreeding season (4). The prostate and the corpus spongiosum enlarge from the end of January and are at their maximum at the end of March and the beginning of April. They have diminished to their minimal size by the end of May.

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Other TALPIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Neurotrichus gibbsii Baird Least Shrew Mole	Feb.–Sept. (Dalquist and Orcutt)		1–4		Western N. America
Scalopus aquaticus L. Common American Mole	Mid to end March, possibly again in June (Arlton)		2–5	About 6 weeks	N. America, east of Rockies

Other TALPIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Scapanus townsendii Bachman Townsend's Mole	Feb. One litter a year (N.A.F. 55)	Late March	2–4, usually 3; mean $3.0 \pm .17$		Northwestern U.S.
Talpa romana Thomas					Constant presence of pluriovular follicles (Bini)

SORICIDAE

Blarina brevicauda Say

MOLE SHREW

The North American short-tailed shrew is sexually active from the first week in February, and the testes reach their greatest development in early April. The young are born from mid-April to the end of May, and probably a second litter may be born in August–September. The male has a side gland which develops with the testes (1). The litter size is 3 to 7, averaging 4.5 (2), but embryo counts from animals caught in the wild have given $6.6 \pm .36$. The duration of pregnancy is 17 to 20 days from the end of sexual receptivity (2).

Ovulation is induced by coitus, and the female is in heat continuously for at least 33 days in the absence of the male. It requires several matings to induce ovulation, and, if sufficient are made, this occurs about 64 hours (55 to 71) from the time of the first mating. The follicles during heat are 0.35 to 0.45 mm. in diameter. The antrum is small and the granulosa cells are large. After copulation the follicles increase slightly in size, and the theca becomes more vascular. Ten hours before ovulation the basement membrane below the granulosa layer disappears. The first polar body is given off, and

luteinization begins to push the ovum and a ball of granulosa cells surrounding it out of the follicle. Spermatozoa often penetrate the ovum before it is extruded from the follicle. The size of the ovum is $70 \times 80\ \mu$. The corpus luteum sometimes has a small cavity at the point of ovulation, and mitoses are frequent in the cells around the edge of the corpus. Its maximum size is 0.75 mm. in diameter, and it degenerates when the embryos are 7 mm. long. By the time of parturition it has almost or entirely vanished. The average number of corpora lutea found was 6.1, and of embryos 5.7 (2).

Pseudopregnancy lasts 9 to 10 days from the time of ovulation. There is no postparturition heat. Internal migration of blastocysts may occur; the ovarian capsule is usually closed (2).

During anestrum the vaginal lumen is usually closed and its lining consists of two layers of epithelial cells. At the time of heat it develops an abrupt flexure, sigmoid in the vertical plane, corresponding to that of the penis. The epithelium becomes stratified, and mitoses are abundant, both in proestrum and in heat. Cornification is well marked, and there is a leucocyte invasion at the end of heat. The vagina is cornified during lactation (2).

During heat the uterine epithelium is tall columnar, with mitoses. Many leucocytes are to be found in the stroma, and they migrate to the lumen after copulation (2).

The oviduct is ciliated at the ovarian end, but few can be found in the mid-region and none at the uterine end. They are entirely absent during anestrum (2).

The penis is sigmoid and has horny ridges or rings on the glans. The testes produce no spermatozoa from November to January, and during this time the penis and accessory organs are small. Growth begins late in January, and by late February spermatozoa may be found. There is less regression in winter in males which are kept in the laboratory than in those obtained from the wild. Both males and females breed in their first year if they are born early enough; puberty in the male is reached in 50 to 80 days. The pectoral scent gland is developed in the spring, more so in the male than in the female. No copulation plug is formed at coitus (2).

1. Hamilton, W. J., Jr. J. Mammalogy, 10: 124–134, 1929.
2. Pearson, O. P. Am. J. Anat., 75: 39–93, 1944.

Sorex aranus L.

COMMON SHREW

The common Old World shrew has a breeding season from May to September or October. The onset of the first heat of the season is gradual, and so is the season's cessation, with a greater number of failures to become pregnant at the postparturition heat occurring as the year advances. Females which do not become pregnant pass into the lactation anestrum without the presence of corpora lutea in their ovaries. Breeding lasts longer in the southern parts of Great Britain than it does toward the north. No condition resembling pseudopregnancy has been observed. The average number of embryos is 6.45, and of corpora lutea 7.35. The litter size declines after July because of increased intra-uterine mortality. The period of gestation lies between 13 and 19 days. Implantation appears to be delayed if the female is lactating (1).

The ripe graafian follicle is 350 μ in diameter and the ovum 72 μ. The corpus luteum has a central cavity for a while, but little blood is found in it. The mature corpus is about 500 μ in diameter, but retrogression sets in before parturition and is marked by the presence of mitoses in the luteal cells. At parturition the diameter is reduced to half. The ovary is surrounded by a closed capsule (1).

Only the lower part of the vagina is closed in immature females. The epithelium is intensely cornified during the first heat, and toward its end there is hyperemia and extravasation of leucocytes, which pass into the lumen. Cornification does not occur in the postparturition heats. The upper and lower parts of the vagina differ, with a circular fold at the point of change. The lower part is thinner and the wall more folded (1).

The uterus has a single cervix, and but little glandular tissue can be found in the endometrium. There is a characteristic fibrous zone between the mucosa and the muscle in the uterus of the nonparous female. The part of the oviduct proximal to the ovary is ciliated. Changes during the cycle are slight, and secretion occurs only while the ova are in transit (1).

Spermatogenesis begins in March and continues at least into November. The prostate is relatively large. The males do not breed in their year of birth; neither do the females, though they tend to display precocious sexual

activity in the fall. They apparently die at the end of their first breeding season (1).

1. Brambell, F. W. R. Trans. Roy. Soc., London, 225B: 1–62, 1935.

Sorex minutus L.

LESSER SHREW

The lesser European shrew begins to breed in mid-April in Great Britain. The season is at its height in June and is over in October. The young do not breed during their first year. The first heat is prolonged, with vaginal cornification and gradual hypertrophy of the sexual organs. The largest follicles average 330 μ in diameter, and the corpora lutea about 475 μ. The latter disappear quickly. There is a postparturient heat, and, if the female does not become pregnant at this time, lactation anestrum follows. Like *S. araneus*, breeding animals do not survive beyond their first season: unlike that species, no fibrous zone is found between the endometrium and the uterine muscle in young females. The average corpus luteum count is 6 to 8, and that of embryos is 6.2 (1).

1. Brambell, F. W. R., and K. Hall. Proc. Zool. Soc., London, 957–969, 1936.

Other SORICIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Blarina telmalestes Merriam Dismal Swamp Shrew	Early spring to late Sept. (Hamilton)	3–7		Virginia
Crocidura caerulea Kerr Indian Musk Shrew	All year (Sansom)			India
C. deserti Schwann Desert shrew	Probably all year (Shortridge)	3–5		S. Africa

Other SORICIDAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
C. occidentalis Pucheran Giant Desert Shrew		4		Africa. One record
Cryptotis parva Say Small Short-tailed Shrew	All year in Florida. March–Nov. further north (Hamilton)	3–6; mean 4.6 ± .22; mode 5		Eastern and southern U.S.
Microsorex hoyi Baird Pygmy Shrew	Several litters a year. Spring and summer (Hamilton)	5–7		N. America
Myosorex varius Smuts		3		S. Africa. One record
Notiosorex crawfordi Coues		3		Southwestern N. America. One record
Sorex arcticus Merriam	Polyestrous (Hamilton)	6–10		Alaska
S. cinereus Kerr Common American Shrew	Polyestrous except in winter (Hamilton)	4–10		Eastern and northern N. America
S. dispar Batchelder Long-tailed Shrew		2		Eastern U.S.
S. fumeus Miller Smoky Shrew	Late March–Aug. Polyestrous (Hamilton)	Av. 5.5	3 weeks or less	Eastern N. America
S. longirostris Bachman		4		Southeastern U.S. One record
S. obscurus Merriam Dusky Shrew	May–Aug. (N.A.F. 55)	4–8, usually 6		Western N. America
S. palustris Richardson Water Shrew	Probably polyestrous (Long)	5–7		Northeastern N. America

Other SORICIDAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
S. vagrans Baird Vagrant Shrew	July–Aug.	6–7		Western N. America

TUPAIIDAE

Tupaia javanica Horsfield

TREE SHREW

The Javan tree shrew is said to experience proestrous bleeding (1), but it is possible that this bleeding and uterine desquamation is menstruation-like in nature (2,3).

1. Stratz, K. H. Der geschlechtsreife Säugethiereierstock. Hague, 1898.
2. Herwerden, M. van. Bijdrage tot de kennis van menstrueelen cyclus en puerperium. Leiden, 1905.
3. van der Horst, C. J., and J. Gillman. South African J. Med. Sci., 6: 27–47, 1941.

GALEOPITHECIDAE

Galeopithecus volans L.

FLYING LEMUR

During proestrum (?) the uterus of the Malayan flying lemur is hyperemic, the capillaries are congested, and blood is extravasated. There is a little local denudation of the epithelium which may occur in any part of the uterus (1). One young is born at a time (2).

1. Herwerden, M. van. Tijdschr. Ned. dierk. Vereen., 10: 1–140, 1906.

2. Blanford, W. T. The Fauna of British India, Including Ceylon and Burma. Mammalia. London, 1889–91.

Other GALEOPITHECIDAE

SPECIES	GESTATION PERIOD
Galeopithecus variegatus Geoffroy Flying Lemur	60 days

CHIROPTERA

BATS living in temperate regions usually have one heat period and one pregnancy a year, but, in the tropics, many species are polyestrous and may have more than one litter a year. The usual number of young is 1 to 2.

The most interesting feature in bats is the fact that, in some species, coitus occurs in the fall and the spermatozoa are retained as a mass in the uterus, remaining immotile until the spring. Ovulation and fertilization then occur. This condition is believed to be peculiar to those bats living in temperate climates which hibernate during the winter. In some vespertilionid bats only one ovary, usually the right, is functional; in others, both appear to be functional, but pregnancies are found only in the right horn of the uterus.

An interesting feature in the males of hibernating species is that the interstitial cells and spermatogenesis appear to have an opposite rhythm, so that, although spermatogenesis ceases in winter, the epididymis and accessory organs are fully developed and spermatozoa are stored until the spring. Thus, although pregnancy may result from spermatozoa stored in the uterus or vagina, renewed insemination in the spring is possible. In these species interesting results might be obtained, especially for the males, if differential assays and cell counts of the anterior pituitary were made at various times of the year.

PTEROPIDAE

Pteropus geddiei MacGillivray

FLYING FOX

This flying fox in the New Hebrides conceives in February and March, or possibly in June and July. The young are born from late August to early

September. There are no pregnancies from November to January. The male is suddenly sexually mature at 600 g. body weight. Spermatogenesis occurs all the year round, but the testes weigh least in July and most in January (1). The interstitial cells of the testes are most numerous and are largest during the month of copulation and for three months previously, i.e., from October to February. From March to June they are moderate in number and size, and in July and August they are at their minimum (2).

1. Baker, J. R., and Z. Baker. J. Linn. Soc. (Zool.), 40: 123–141, 1936.
2. Groome, J. R. Proc. Zool. Soc., London, 110A: 37–42, 1940.

Pteropus giganteus Bruenn

INDIAN FRUIT BAT, FLYING FOX

The Indian fruit bat has young at any time of the year in the London Zoo. In India the young are born from the end of March to the end of April, but in Ceylon they are born later (1). Copulation has been observed on January 25, in India. In February a single embryo each was found in females which had been shot (2).

1. Baker, J. R., and Z. Baker. J. Linn. Soc. (Zool.), 40: 123–141, 1936.
2. McCann, C. J. Bombay Nat. Hist. Soc., 42: 587–592, 1941.

Other PTEROPIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Cynopterus brachyotis Müller Short-nosed Fruit Bat		Sept. (Baker)		India and Borneo
Eidolon helvum Kerr		Feb.–March (Baker)		Equatorial Africa
Epomophorus angolensis Gray Angola Fruit Bat		Sept.–Oct. (Shortridge)	1, rarely 2	S. Africa

Other PTEROPIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
E. crypturus Peters		Oct. (Baker)		E. Africa
E. wahlbergi Sundevall Epauletted Fruit Bat			1	Cent. Africa
Epomops dobsonii Bocage Epaulette Bat			2	Angola
Macroglossus lagochilus Matschie		Aug. (Baker)		India
Pteropus ariel G. M. Allen		April (Baker)		
P. conspicillatus Gould	March (Baker)			Australia
P. eotinus Andersen	Feb.–Mar. or June–July (Baker)	Late Aug. to early Sept.		New Hebrides
P. gouldi Peters	March–April (Baker)	Sept.–Oct.		N. Australia
P. melanotus Blyth	Oct. (Baker)	Feb.–March		Nicobar Is.
P. niger Kerr	End Oct. (Baker)			Reunion
P. poliocephalus Temminck Red-necked Fruit Bat	March–April (Ratcliffe)	Oct.	1	Australia
P. rufus Geoffroy			2	Madagascar
P. scapulatus Peters	Oct. (Baker)	April		Queensland

Other PTEROPIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
P. subniger Kerr	May (Baker)	End Oct.		Reunion
Rousettus aegyptiacus Geoffroy	All year in Egypt in captivity; in wild Sept.–Oct. (Baker)	Feb.–March	1	N.E. Africa and S.W. Asia
R. leachii A. Smith		Feb.–Oct. in London Zoo (Baker)		Cent. and S. Africa

EMBALLURONIDAE

Coleura afra Peters

This East African bat has the ovaries completely enclosed by capsules. It also has a well-developed female prostate. One female had a single embryo (1).

1. Matthews, L. H. Proc. Zool. Soc., London, 111B: 289–346, 1941.

Other EMBALLURONIDAE

SPECIES	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Peropteryx canina Wied		1 always	Cent. America and northern S. America
Rhynchiscus naso Wied		1 always	Cent. America

Other EMBALLURONIDAE (*Continued*)

SPECIES	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Saccopteryx bilineata Temminck Lesser White-lined Bat		1 always	Cent. America and northern part of S. America
Taphozous longimanus Hardwicke Long-armed Sheath-tailed Bat	Pregnant in August (Blanford)	1	India

NOCTILIONIDAE

Noctilio leporinus L.

This bat, which lives in the northern part of South America, Central America, and the West Indies, bears 1 young at a time.

PHYLLOSTOMIDAE

Glossophaga soricina Pallas

This bat, a native of South America, breeds late in the spring, shortly before the rains. There is one heat period a year. The breeding season lasts for 2 to 3 weeks, and ovulation is at this time. A nonpregnant female with a corpus luteum bleeds from a degenerating hypertrophied endometrium. This bleeding is believed to occur at the end of pseudopregnancy (1).

1. Hamlett, G. W. D. Anat. Rec., 60: 9–17, 1934.

Other PHYLLOSTOMIDAE

SPECIES	BREEDING SEASON	NO. OF BIRTH	SEASON OF YOUNG	HABITAT, ETC.
Artibeus jamaicensis Leach			I	Cent. America and West Indies. Uterus simplex with oviducts near mid-line (Wislocki and Fawcett)
A. nanus Andersen			I	Mexico. One record
Carollia perspicillata L. Short-tailed Bat	Pregnant Aug. and Jan. in Amazon Valley (Hamlett)	March in Panama (Enders)	I	Cent. and S. America
Erophylla planifrons Miller			I	S. America and West Indies. One record
Macrotus californicus Baird		June (Burt)	I	Southwestern N. America
Phyllonycteris poeyi Gundlach		June–July	I	West Indies

NYCTERIDAE

Nycteris hispida Schreber

This bat of central and West Africa has an incomplete capsule around the ovary and very few glands in the endometrium. The separate cervical canals open on a single cervix in the vagina. The lumens of the canals contain no glands. The young are born early in December, and there is probably another pregnancy shortly afterwards but not so soon as in *N. luteola.* There is very little erectile tissue in the penis (1).

1. Matthews, L. H. Proc. Zool. Soc., London, 111B: 289–346, 1941.

Nycteris luteola Thomas

In this central and East African bat the ovaries are enclosed in capsules, each with a large lateral slit. The cortex is thin except at the poles, and the graafian follicles are crowded together at these points. When ripe, the follicles are 400 μ in diameter, with a large antrum. The subepithelial coat of the vagina is in long folds and the epithelium above them forms a uniform coat which, therefore, varies from 100 to 35 μ in thickness. This becomes immensely thickened and is cornified during heat. The oviducts are very coiled and tortuous. The endometrium contains few glands. The females are probably polyestrous and have more than one pregnancy a year. These occur in quick succession. There is no trace of a corpus luteum in the ovary during pregnancy after an early stage. One young is born at a time (1), and the female has a postparturient heat (2).

The penis is covered with long, stiff hairs directed caudally. The prostate has lateroposterior parts only (1).

1. Matthews, L. H. Proc. Zool. Soc., London, 111B: 289–346, 1941.
2. Matthews, L. H. Nature, 143: 643, 1939.

Other NYCTERIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Nycteris borealis Müller Northern Red Bat	Aug. (Hamilton)	Late May to mid-June	2–4; mode 3, mean 3.00 ± .06	Northern Eurasia and America
N. capensis A. Smith Cape Slit-faced Bat		Pregnant Oct. (Shortridge)	1	S. Africa
N. cinerea Peale and Beauvois Hoary Bat	Early Aug. (Seton)	Mid-June to early July (Hamilton)	2	N. America

MEGADERMIDAE

Cardioderma cor Peters

This Abyssinian big-eared bat has a penis covered with hairs. The organ also has a remarkable caudal curvature. The female usually has one young, and the corpus luteum is exceptionally large. In each of two specimens examined there was one fetus and two corpora lutea, one on each side (1).

1. Matthews, L. H. Proc. Zool. Soc., London, 111B: 289–346, 1941.

Other MEGADERMIDAE

SPECIES	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Lyroderma lyra Geoffroy Indian Vampire Bat	Pregnant Feb. (Blanford)	1	India and China
Megaderma spasma L. Malay Vampire Bat	May (Allen)		S.E. Asia

RHINOLOPHIDAE

Rhinolophus ferrum-equinum Schreber

GREATER HORSESHOE BAT

The European horseshoe bat is in heat toward the end of October, and it copulates at this time. Spermatozoa are stored in the uterus and vagina throughout the winter. Ovulation occurs in mid-April (1). There is also said to be a spring copulation, so the question whether or not conception can result from a fall copulation has not yet been settled (2).

The ovary is enclosed in a capsule, and the right ovary only is functional;

consequently, pregnancy is always on the same side. The mature follicle measures 350 μ and the ovum 70 μ. The corpus luteum is buried in the ovary. When the bat is in heat, toward the end of October, the vaginal epithelium becomes cornified, but the follicles do not reach their maximum size until the time of ovulation. A copulation plug is formed by means of which most of the spermatozoa are stored until April, when the plug breaks up and is expelled. At the same time the vaginal epithelium, which has remained cornified, is desquamated. The corpus luteum is large and is not completely resorbed until near the end of lactation. Only one egg is released at a time, and one young is born in late June and July. Females have only one heat period in a year, and are 15 months old at the beginning of their first heat. The males are sexually mature at about the same time. The young are usually born in June (1).

Graafian follicles are present in the nonfunctional left ovary, but they degenerate and do not rupture (1).

The testes are active throughout the winter, and the spermatozoa are said to be stored in the female throughout this period in a pocket on the ventral surface of the vagina (3).

Ovulation and fertilization may be produced in January by the injection of a gonadotrophic extract of the pituitary gland (4).

1. Matthews, L. H. Trans. Zool. Soc., London, 23: 213–255, 1937.
2. Baker, J. R., and Z. Baker. J. Linn. Soc. (Zool.), 40: 123–141, 1936.
3. Rollinat, R., and E. L. Trouessart. Compt. Rend. Soc. Biol., Paris, 52: 604–607, 1900.
4. Herlant, M. Bul. Acad. Roy. de Belgique, 20: 359–366, 1934.

Rhinolophus hipposideros Bechstein

LESSER HORSESHOE BAT

As this European bat mates in the fall and not in the spring, probably the spermatozoa are stored in the female tract throughout the winter (1). The young are born in late June and July (2).

The mature follicle measures 300 μ, and the ovum 70 μ. The corpus luteum is attached to the ovary by a peduncle (3).

In the male spermatogenesis begins in July, and the interstitial cells and accessory organs are in an active state. In October spermatogenesis has ceased,

but the interstitial cells are still active, while the accessory organs are more so than they were in July. In winter there is no spermatogenesis, the interstitial cells are voluminous but not as vacuolated as in October, and the accessory organs continue to be well developed (4).

1. Baker, J. R., and Z. Baker. J. Linn. Soc. (Zool.), 40: 123–141, 1936.
2. Barrett-Hamilton, G. E. H. A History of British Mammals. London, 1910.
3. Matthews, L. H. Trans. Zool. Soc., London, 23: 213–255, 1937.
4. Courrier, R. Arch. de Biol., 37: 173–334, 1927.

Other RHINOLOPHIDAE

SPECIES	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Rhinolophus geoffroyi A. Smith		1, rarely 2	Cent. and S. Africa
R. perniger Hodgson Great Indian Horseshoe Bat		1	India
R. rouxi Temminck	April–May (Allen)		S. and S.E. Asia
R. tragatus Hodgson	Once a year, toward end of summer (Blanford)	2	India

HIPPOSIDERIDAE

Hipposideros caffer Sundevall

In this African bat the penis is curved and has hairs. The vas deferens has a conspicuous ampulla which is a blind diverticulum. The urethral glands are very well developed (1).

1. Matthews, L. H. Proc. Zool. Soc., London, 111B: 289–346, 1941.

Triaenops afer Peters

This bat, which is indigenous to Kenya, has one young at a time. No corpus luteum could be found in pregnant specimens, but the amount of ovarian stroma was slightly increased. The ovarian capsule is not closed, and the oviduct has a double sigmoid curve. The glans penis has flattened lobes. There is no scrotum (1).

1. Matthews, L. H. Proc. Zool. Soc., London, 111B: 289–346, 1941.

Other HIPPOSIDERIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Hipposideros armiger Hodgson Great Himalayan Leaf-nosed Bat	Once a year (Blanford). Probably Aug. (Hinton and Lindsay)	Toward end of summer	2	India. Male has very strong odor, absent in female
H. bicolor fulvus Gray				India. Female has vivid coloration in breeding season (Barrett-Hamilton)

VESPERTILIONIDAE

Eptesicus fuscus Peale and Beauvois

BIG BROWN BAT

The North American brown bat mates in the fall, and the young are born in mid-June toward the north of its range, but earlier in the south (1). There is no doubt that spermatozoa survive in the uterus throughout the winter, since females collected in December, kept in isolation at 40° F., and autopsied in May after a month at 75° F. were found to contain embryos. The sper-

matozoa had survived for at least 140 to 150 days (2). In 30 cases observed the number of blastocysts varied from 1 to 6, with an average of 3.9 and a mode of 4 (3). The number of young varies from 1 to 4, but all authorities agree that 2 is the usual number.

The ovaries are small, rounded, and without a neck (4). The average number of follicles, which enlarge during hibernation or which rupture, is 4.2, and they are present in each ovary in almost equal numbers, 53 per cent in the left. It is impossible to differentiate between theca interna and theca externa in the follicle wall. The granulosa cells begin to luteinize before ovulation, and there is a decrease in the amount of follicular fluid, which penetrates the theca. Rupture is sudden, but there is very little hemorrhage. It is usual to find a cavity in the corpus luteum (5).

In December there are a few spermatozoa in the testes, but no spermatocytes or spermatids. At this time, also, the uterus contains a mass of spermatozoa, but there are none in the oviducts (6).

1. Hamilton, W. J., Jr. The Mammals of Eastern United States. Ithaca, 1943.
2. Wimsatt, W. A. Anat. Rec., 83: 299–306, 1942.
3. Wimsatt, W. A. Anat. Rec., 88: 193–204, 1944.
4. Guthrie, M. J. J. Mammalogy, 14: 199–216, 1933.
5. Wimsatt, W. A. Am. J. Anat., 74: 129–173, 1944.
6. Evans, C. A. Am. Nat., 72: 480–484, 1938.

Eptesicus serotinus Schreber

SEROTINE BAT

This Old World bat copulates in September in France (1), and not again in the spring (2). But the testes begin to hypertrophy in May and spermatogenesis commences. In June spermatozoa are present and spermatogenesis continues until September. The epididymis is full of spermatozoa throughout hibernation, and the accessory organs are well developed as well as the interstitial tissue of the testis. In May the epididymis diminishes in size, the accessory organs atrophy, and the interstitial cells are pigment laden. In June the condition is the same except that pigment can no longer be found in the interstitial cells, which appear to be fully active by August and September (1). It would seem, therefore, that insemination is possible

for a great part of the year in spite of the belief that it only occurs in the fall. The number of young, born late in May, is usually one.

Castration of males in December and continuation of hibernation had no effect upon the epididymis and sperm storage during that season. The accessory organs remained active whether or not the epididymides were removed during the operation. But exposure of the castrated bats to higher temperatures, while not affecting the epididymis and spermatozoa, caused the accessory glands to atrophy. A castrate liberated and caught during the next hibernating season showed the usual castrate atrophy of the whole reproductive tract (1).

Females injected with a pituitary gonadotrophe in December ovulated 4 days afterwards. A similar experiment done in January was followed by pregnancy (3).

1. Courrier, R. Arch. de Biol., 37: 173–334, 1927.
2. Baker, J. R., and T. F. Bird. J. Linn. Soc. (Zool.), 40: 143–161, 1936.
3. Herlant, M. Bul. Acad. Roy. de Belgique, 20: 359–366, 1934.

Miniopterus australis Tomes

In the New Hebrides this bat copulates at the end of August or the beginning of September, i.e., in the spring, and the development of the embryo begins at once. One embryo develops and it is nearly always in the right horn. The testes are small in September, but spermatozoa are still in the epididymis, from which they disappear by December. In April the testes begin to grow, and by August they attain their maximum weight (1).

1. Baker, J. R., and T. F. Bird. J. Linn. Soc. (Zool.), 40: 143–161, 1936.

Miniopterus minor Peters

This bat from Zanzibar has its young earlier than December, the usual time of pregnancy for other species from the same caves. The ovarian capsules

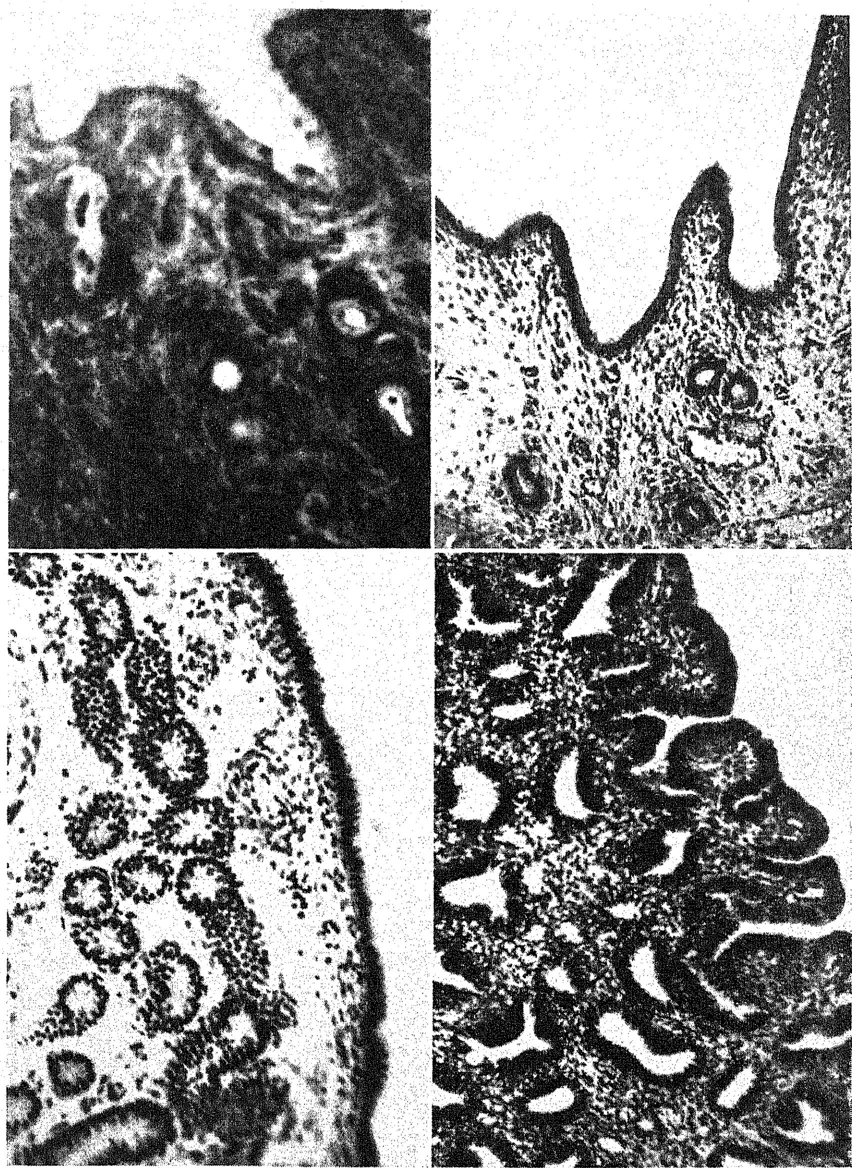

PLATE V. Types of uterine changes with cycle. *Upper left:* Rat in heat. *Upper right:* Rat in diestrum, slight glandular change with functioning corpus luteum. H and E. x100. *Lower left:* Pig in diestrum, moderate glandular change, iron hematoxylin. x100. (Taken from a slide prepared by Dr. G. W. Corner.) *Lower right:* Rabbit in pseudopregnancy, extreme glandular change. H and E. x100.

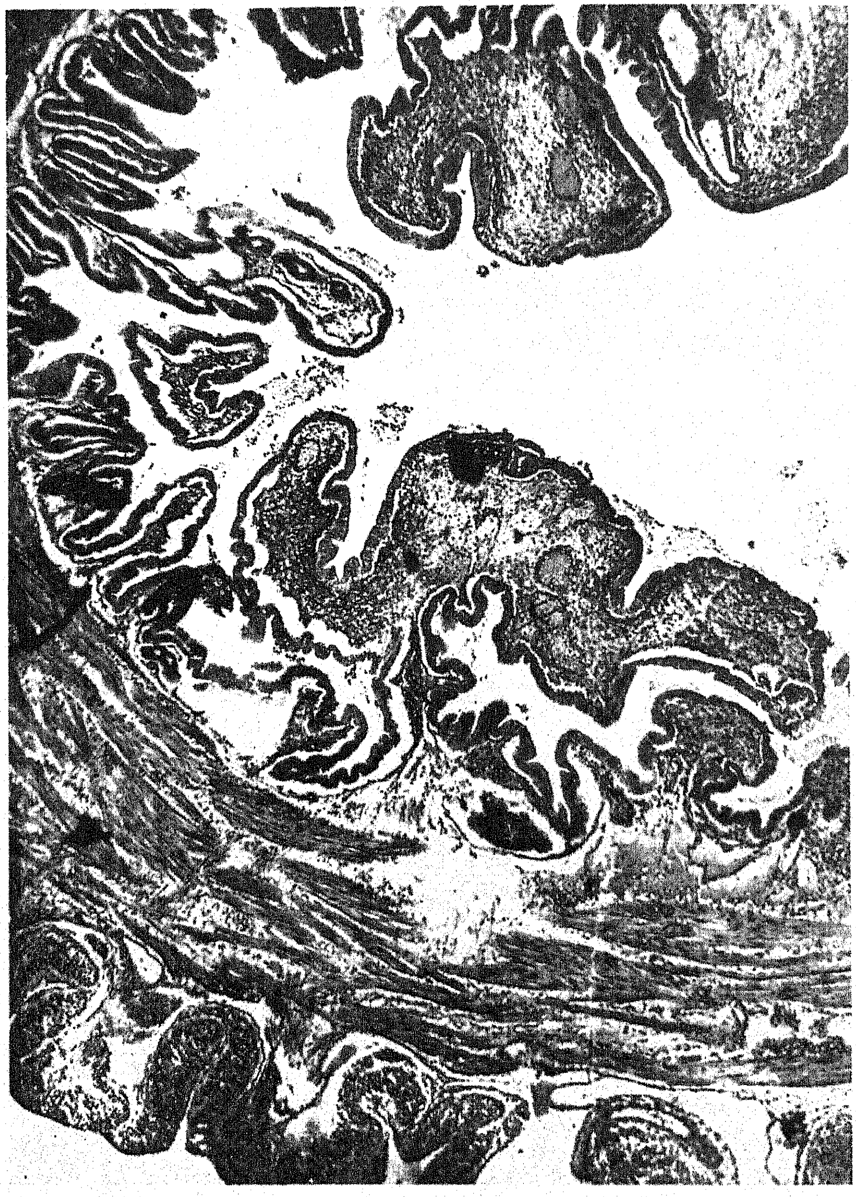

Plate VI. Uterus of *Microtus pennsylvanicus*, pseudopregnancy immediately after parturition. This photograph is taken of a section of uterus from a field mouse early in pseudopregnancy immediately following parturition. It represents an unusual type in which the uterus has not yet recovered from pregnancy and is included to illustrate the need for caution in interpreting sections.

are open. The cornua are almost at right angles to the body of the uterus. The vaginal epithelium mucifies during pregnancy (1).

1. Matthews, L. H. Proc. Zool. Soc., London, 111B: 289–346, 1941.

Miniopterus natalensis A. Smith

This bat, a native of South Africa, has the ovary enclosed in a capsule with a small opening. The ovarian stroma contains much interstitial tissue. The corpus luteum is large and, when young, has a blood clot in the center. One young is born at a time, and in 8 pregnant females all the embryos were in the right horn of the uterus and all the corpora lutea in the left ovary (1). This unusual condition needs confirmation.

The glans penis is minute; the vas deferens has an enlarged ampulla consisting of a mass of connective tissue with numerous diverticula. The prostate is large (1).

1. Matthews, L. H. Proc. Zool. Soc., London, 111B: 289–346, 1941.

Miniopterus schreibersii Kuhl

This bat, a native of southern Europe and Algeria, ovulates in October or November and mates and is fertilized at that time. Ovulation is almost invariably from the right ovary (1).

In August the testes are in full spermatogenesis; in September this condition has ceased, but the interstitial tissue is well developed and the accessory organs are very active. The epididymis is very voluminous and is full of spermatozoa. In November some testes have retrogressed while others are still well developed, but, although spermatozoa are present, their formation has ceased. The interstitial tissue is reduced. This state continues into January and April, but the number of spermatozoa diminishes. In April, however, the interstitial tissue is showing signs of recovery. At the time of fertilization the testes are inactive and the spermatozoa must, therefore, come from the epididymis (1).

1. Courrier, R. Arch. de Biol., 37: 173–334, 1927.

Myotis austroriparius Rhoads

RHOADS' BAT

This bat, indigenous to eastern United States, which is sometimes classed as a subspecies of *M. lucifugus* Le Conte, has 1 to 2 young, which are born during the first half of May. Records give an average of 1.7 ± .06 and a mode of 2 (1). The young at birth are extruded into a pocket formed by the interfemoral and alar membranes. They remain attached to the mother by the umbilical cord for several hours (2).

1. Sherman, H. B. J. Mammalogy, 11: 495–503, 1930.
2. Hamilton, W. J., Jr. The Mammals of Eastern United States. Ithaca, 1943.

Myotis capaccinii Bonaparte

In this bat of southern Europe and northwestern Asia spermatogenesis has ceased by November, but the epididymis is full of spermatozoa. The interstitial cells of the testis are variable, and the accessory organs are hypertrophied, though involution is beginning. In April some spermatozoa are still present, but the epididymis and accessory organs are in the resting state, while the interstitial cells are vacuolated (1).

1. Courrier, R. Arch. de Biol., 37: 173–334, 1927.

Myotis grisescens Howell

GRAY BAT

The gray bat of eastern North America mates in the fall, and one young is born in early June to early July (1). The females have spermatozoa in the uterus in September, October, November, and December, the only months in which they were examined. The ovary is somewhat oval, and the round ligament is pigmented. One ovum is matured at a time, and its size (tubal) is 116 μ in diameter (2). Spermatogenesis occurs in the summer when the

rest of the reproductive tract is quiescent. The epididymis is full of spermatozoa in fall, winter, and spring, and the accessory organs are full of secretion. The interstitial cells are largest in summer, retrogress in the fall, and remain small until spring. The male is sexually mature in its second summer (3).

1. Hamilton, W. J., Jr. The Mammals of Eastern United States. Ithaca, 1943.
2. Guthrie, M. J. J. Mammalogy, 14: 199–216, 1933.
3. Miller, R. E. J. Morphol., 64: 267–295, 1939.

Myotis lucifugus Le Conte

LITTLE BROWN BAT

The little brown bat of North America east of the Rocky Mountains has been much investigated, and the survival of spermatozoa in the uterus throughout the winter and fertilization by these spermatozoa in the spring have been proved beyond doubt.

Copulation occurs in the wild both in the fall and in spring. One young is born at a time, in mid-June to mid-July (1). The sex ratio at birth is 50.6 per cent males (2). Spermatozoa survived in the uteri of females isolated in a refrigerator throughout the winter for at least 159 days, and cleaving eggs and blastocysts were found in the uteri in spring (3).

The theca of the graafian follicle does not divide into interna and externa. The large follicle during hibernation measures about 350 μ in diameter and the cells of the discus proligerus are hypertrophied. Just before ovulation, in spring, the antrum almost disappears, the volume of liquor folliculi decreases, and there is a preovulatory luteinization of the granulosa cells accompanied by a progestational reaction in the uterus. The wall of the rupturing follicle folds only to a small extent, and a cavity in the corpus luteum is rare. Ovulation occurs in late April or early May, during the passage from hibernation to summer quarters. When the females are kept in a warm laboratory, it is advanced to the middle of February. The diameter of the ovum is about 80 μ (4). The females reach sexual maturity at the end of their first summer. The embryo always develops in the right horn of the uterus (5), but the ripe follicle or corpus luteum is in the corresponding ovary in only 48 per cent of cases (4), or 49 per cent (6). In first-season females

there is a preponderance of ripe follicles in the left ovary. The ovary is rounded and has a very inconspicuous neck (5).

In October the vaginal epithelium consists of many layers, but desquamation is continuous throughout the winter with the result that its thickness is reduced by April. In August intensive cornification sets in. The condition throughout hibernation may be described as one of submaximal estrus (7).

The round ligament of the uterus is not pigmented, in contrast to the condition in *M. grisescens* (5). The height of the epithelium is medium in October, and it is lowest in February. The uterine and glandular epithelia hypertrophy after ovulation so that the glandular epithelium appears to be irregular. The epithelium throughout is nonciliated and of a secretory type (7).

The tubal epithelium is ciliated and secretory. It is highest in October, is vacuolated during winter, and recovers in the spring. After ovulation, it is low and nonsecreting (7).

Spermatogenesis is in summer when the rest of the reproductive tract is quiescent. The epididymis is full of spermatozoa from fall to spring; the accessory organs are full of secretion and remain so until April. The interstitial cells are at their maximum size in summer, retrogress during the fall, and remain small until spring. The male is sexually mature in its second summer (8).

1. Hamilton, W. J., Jr. The Mammals of Eastern United States. Ithaca, 1943.
2. Griffin, D. R. J. Mammalogy, 21: 181–187, 1940.
3. Wimsatt, W. A. Anat. Rec., 88: 193–204, 1944.
4. Wimsatt, W. A. Am. J. Anat., 74: 129–173, 1944.
5. Guthrie, M. J. J. Mammalogy, 14: 199–216, 1933.
6. Guthrie, M. J., and K. R. Jeffers. Anat. Rec., 71: 477–496, 1938.
7. Reeder, E. M. J. Morphol., 64: 431–453, 1939.
8. Miller, R. E. J. Morphol., 64: 267–295, 1939.

Myotis myotis Bechstein

(=*Vespertilio murinus* L.)

COMMON EUROPEAN BAT

This bat mates in mid-September (1) and again in spring (2). Ovulation is at the end of March, and the length of gestation is 50 days (1). One young

is born at a time, and the embryo is nearly always in the right horn of the uterus (2), but the corpora lutea are in the right ovary in only 55.7 per cent of cases (3). Throughout winter spermatozoa may be found clinging to the uterine wall (4).

Spermatogenesis begins in May, when there are few spermatozoa in the epididymis; the interstitial cells appear to be active, but the accessory organs are large. The interstitial cells are pigmented. From December to February spermatogenesis has ceased, spermatozoa are present in the epididymis, the interstitial tissue is variable, and the accessory organs are well developed though there is some retrogression, less in the seminal vesicles than in the epididymis and prostate (1).

1. Courrier, R. Arch. de Biol., 37: 173–334, 1927.
2. Baker, J. R., and T. F. Bird. J. Linn. Soc. (Zool.), 40: 143–161, 1936.
3. Duval, M. J. de l'Anat., 31: 93–160, 1895.
4. Redenz, E. Zeit. Wiss. Biol., Abt. B., Zeit. Zellforsch u. Mikros. Anat., 9: 734–739, 1929.

Myotis sodalis Miller and Allen

This North American bat mates in September or October, and spermatozoa can always be found in the uterus from October to February (1). Spermatozoa have survived in the uteri of isolated females for up to 135 days at least (2). The ovary is lobed and matures one ovum at a time. Ovulation in the laboratory under warm conditions has occurred in the middle of February. The round ligament is pigmented (1).

1. Guthrie, M. J. J. Mammalogy, 14: 199–216, 1933.
2. Wimsatt, W. A. Anat. Rec., 88: 193–204, 1944.

Myotis subulatus Say

From a physiological standpoint the nomenclature of this western North American bat probably needs revising. *Myotis subulatus subulatus* Say has 2

as the usual number of young (1), while *M. subulatus melanorhinus* Merriam has 1 (2). Subspecies conform so regularly in their litter sizes that the incorporation of these two into one species is open to question.

1. Bailey, V. North American Fauna, No. 49, 1926.
2. Bailey, V. North American Fauna, No. 53, 1931.

Nyctalus noctula Schreber

This Old World bat copulates in September. Afterwards the cornified epithelium of the upper vagina sloughs off and forms a plug, which remains in place throughout hibernation (1). In Germany the young are born in early May. One is said to be the usual number in England, but on the Continent 1 and 2 are born at approximately equal numbers of births (2,3). The period of gestation is probably about 49 days (4).

1. Grosser, O. Verh. d. Anat. Gesellsch., 17: 129–132, 1903.
2. Allen, G. M. Bats. Cambridge, Mass., 1939.
3. Vogt, C. Compt. Rend. Assn. Adv. Sci., 655–662, 1881.
4. Barrett-Hamilton, G. E. H. A History of British Mammals. London, 1910.

Pipistrellus abramus Temminck

ASIATIC PIPISTRELLE BAT

In this bat spermatogenesis begins at the end of spring and ceases by October. From October to June the tubules are in repose, but spermatozoa are stored in the tail of the epididymis from October to May. After copulation in the fall the spermatozoa remain immotile in a mucous plug (1). Two young are usually born in a litter (2).

1. Nakano, O. Folia Anat. Jap., 6: 777–828, 1928.
2. Blanford, W. T. The Fauna of British India, Including Ceylon and Burma. Mammalia. London, 1888–91.

Pipistrellus pipistrellus Schreber

COMMON PIPISTRELLE

This common bat of Europe and Asia is said to copulate both in the fall and in the spring (1). The female mates in September, and spermatozoa may be found in the uterus until March. They cling to the uterine wall, and, since the glands are actively secreting during this time, they may derive nourishment from this source. Ovulation in France occurs in March and April (2), but in England it is said not to occur until May. No vaginal plug is formed, and the spermatozoa are stored in the uterus until after ovulation, when many are expelled. The female usually bears one young, and although ovulation may occur from either ovary, one writer has found that the pregnancy was in the right horn in 70 per cent of cases, 25 per cent were in the left, and the remaining 5 per cent were pregnant in both horns. When the embryo is in the horn opposite to the corpus luteum, transfer has been by migration across the body of the uterus (3).

The period of gestation is said to be about 44 days (3), but, as birth in France occurs in July to August while ovulation is said to be in March to April (2), its duration is still an open question. The female reaches puberty in her second year (3).

In the fall the vaginal epithelium becomes hyperplastic and keratinized, and it remains so all winter. The cornified tissue becomes so thick that the lumen is practically blocked during this period, which resembles a prolonged proestrum. Large graafian follicles can be found throughout, but they do not mature until near ovulation time (2).

The male does not reproduce until it is 2 years old. In mid-June spermatogenesis begins, but by the end of August it has ceased. The testes become smaller and by October they reach their minimum weight. The epididymis is small in August and enlarges in October, when its tail is larger than the testis and is full of spermatozoa. It regresses from May onward, and any remaining spermatozoa are phagocytized. The seminal vesicles and prostate are large from the end of August to December. In spring their involution is rapid, and at this time the epididymis is also regressing. The cycle of the interstitial cells is similar. Development begins in June and is at a maximum

in August. They are still well developed in winter and appear to be glandular. In April involution sets in and the cells become pigmented (4).

A case has been described in which full spermatogenesis occurred at the usual time but in which the accessory organs remained atrophic. The interstitial cells of the testis were replaced by lymphoid cells (5).

1. Baker, J. R., and T. F. Bird. J. Linn. Soc. (Zool.), 40: 143–161, 1936.
2. Courrier, R. Compt. Rend. Soc. Biol., Paris, 87: 1365–1366, 1922.
3. Deansley, R., and T. Warwick. Proc. Zool. Soc., London, 109A: 57–60, 1939.
4. Courrier, R. Arch. de Biol., 37: 173–334, 1927.
5. Courrier, R. Compt. Rend. Assn. Anat., 21: 176–182, 1926.

Pipistrellus subflavus Cuvier

This bat of the eastern and southern United States is said probably to mate in August (1), but copulation has been observed in Indiana at the end of November (2), and it is said also to copulate in spring (3). Captured females all had spermatozoa in their uteri between November 11 and April 30. In the warm laboratory ovulation first occurred about March 7 (4). In the southern part of the range, birth is in late May, but further north it extends to late June and mid-July (1).

The ovary is rounded and has no neck. The number of mature follicles or tubal eggs was found to be $4.3 \pm .1$, mode 4 (4); but embryo counts have given 1 to 3, mode 2, means $1.9 \pm .06$; consequently, the loss of eggs or degree of early embryonic atrophy must be high.

1. Hamilton, W. J., Jr. The Mammals of Eastern United States. Ithaca, 1943.
2. Hahn, W. L. Biol. Bul., 15: 135–164, 1908.
3. Baker, J. R., and T. F. Bird. J. Linn. Soc. (Zool.), 40: 143–161, 1936.
4. Guthrie, M. J. J. Mammalogy, 14: 199–216, 1933.

Plecotus auritus L.

LONG-EARED BAT

The reproductive cycle in this Old World bat is essentially similar to that of other hibernating species. Spermatogenesis is at its height in August, and

the interstitial cells of the testis are large at that time (1). It does not occur in spring, and spermatozoa survive throughout the winter in the uterus (2). Copulation is said to take place only in the fall (3). The young, one usually, are born in June and July (4).

1. Courrier, R. Arch. de Biol., 37: 173–334, 1927.
2. Redenz, E. Zeit. Wiss. Biol., Abt. B., Zeit. Zellforsch u. Mikros. Anat., 9: 734–749, 1929.
3. Baker, J. R., and T. F. Bird. J. Linn. Soc. (Zool.), 40: 143–161, 1936.
4. Barrett-Hamilton, G. E. H. A History of British Mammals. London, 1910.

Other VESPERTILIONIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Antrozous pallidus Le Conte Pale Bat		End June to early July (N.A.F. 55)	1–2, in equal numbers	Southwestern N. America
Corynorhinus macrotis Le Conte			1	Southeastern U.S.
C. rafinesquii Lesson Big-eared Bat	Aug., embryos in Sept. and Oct. (N.A.F. 55)	June 15–30	1	N. America
Dasypterus floridanus Miller		May–June (Lowery)	2, rarely 3	Southeastern U.S.
D. ega Peters			2	Mexico and Cent. America
Eptesicus capensis A. Smith Cape Serotine Bat	Embryos in Nov. in S.W. Africa (Shortridge)		2	Africa
Kerivoula lanosa A. Smith			2	S. Africa
Lasionycteris noctivagans Le Conte Silvery Bat	Late Aug. to early Sept. (Seton)	Early June	1–2, usually 2	N. America
Myotis bechsteinii Leisler		Early May	1	Europe

Other VESPERTILIONIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
M. californicus Audubon and Bachman Little Californian Bat		June (N.A.F. 55)	1	Western U.S.
M. chiloensis Waterhouse		Nov. (Lataste)	1	S. America
M. daubentoni Kuhl		June–July (Barrett-Hamilton)	1	Europe
M. evotis H. Allen			1	Western N. America
M. keenii Merriam		July (Hamilton)	1	
M. mystacinus Leisler Whiskered Bat		June–July	1	W. Europe
M. natteri Kuhl		Late June–early July (Barrett-Hamilton)	1	Europe
M. thysanodes Miller		End June or July	1	Southwestern N. America
M. volans H. Allen			1	Western N. America
M. yumaensis H. Allen Tejon Bat		June–July, mostly June, (N.A.F. 55). May in Texas (Bailey)	1	Western N. America
Nyctalus leisleri Kuhl		Late June (Barrett-Hamilton)	1	Europe
Nycticeius humeralis Rafinesque Evening Bat	Aug. (Hamilton)	End May to early June	1–2, usually 2	Eastern and southern U.S.

Other VESPERTILIONIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Pipistrellus fouriei Thomas		Pregnant in Oct. (Shortridge)	2	S.W. Africa. One record
P. hesperus H. Allen Little Canyon Bat		July (N.A.F. 55)	Usually 2	Western N. America
P. kuhlii Natterer White-bordered Bat			2	Southern Europe and Asia, N. Africa
Scotophilus kuhlii Leach				India. Underside of pregnant female changes from pale straw to rich saffron
S. nigrita Schreber Yellow Bat			1–2	Africa
Vespertilio discolor Natterer Particolored Bat			2	Northern Europe and Asia

MOLOSSIDAE

Eumops californicus Merriam

The males of this southern Californian bat have glands on the lower part of the throat which enlarge during the breeding season. They are active from December to March and subside by mid-April. One young is born at a time (1). The oviduct joins the uterus at an angle of 120 degrees. It enters by a papilla which is muscular and nonglandular (2).

1. Howell, A. B. J. Mammalogy, 1: 111–117, 1919.
2. Andersen, D. H. Am. J. Anat., 42: 255–305, 1928.

Tadarida cynocephala Le Conte

FREE-TAILED BAT

In Florida this free-tailed bat mates in mid-February to late March, at ovulation time. One young is born in late May to late June after a gestation of 11 to 12 weeks. The females are sexually mature at 9 months old. The males have a short rutting season, from February to mid-April (1). The cells of the discus proligerus do not hypertrophy as they do in *Myotis lucifugus* (2).

Fairly large graafian follicles are present in the ovaries at all times of the year except when small embryos are present, i.e., for about 2 weeks following ovulation. These are almost always in the right ovary only. Spermatozoa are not stored in the uterus throughout winter and are found only from mid-February to March. The single embryo is almost invariably in the right horn. In the male spermatozoa are present in the testes and epididymis in February and March. Atrophy occurs in April and lasts until September, when proliferation begins in the testes tubules. No spermatozoa, however, can be found until the end of January, but they have not yet reached the epididymis (3).

1. Hamilton, W. J., Jr. The Mammals of Eastern North America. Ithaca, 1943.
2. Wimsatt, W. A. Am. J. Anat., 74: 129–173, 1944.
3. Sherman, H. B. J. Mammalogy, 18: 176–187, 1937.

Other MOLOSSIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Eumops bonariensis Peters			2	Argentina
Tadarida femorosacca Merriam Pocketed Free-tailed Bat			1	California
T. macrotis Gray Free-tailed Bat			1	Cuba

Other MOLOSSIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
T. mexicana Saussure Mexican Free-tailed Bat	Spring (Baker and Bird)	May–June or July, rarely Aug. (Burt)	1	

PRIMATES

THE main inquiry in regard to primate reproduction has centered around menstruation and its significance. This has been discussed in the introductory part of this book. Our knowledge of the lower primates, especially of the Lemuroidea, is very scanty, and, as a means of providing links in reproductive behavior between the higher primates and other mammals, work on these forms is highly desirable. There is some suggestion of a restricted breeding season in many of the lower forms and of varying intensity of reproduction with the season in some of the higher ones. Also, bleeding into the uterine cavity, often of small amount, at the end of the life of the corpus luteum appears to be widespread, but it is not sufficient in quantity to produce overt menstruation except in the Old World primates. The smaller amount of bleeding implies that there is less tissue destruction in the endometrium. The reader should refer to the work upon the elephant shrew (*Elephantulus*) in the Insectivora for a possible connecting link between primates and other species.

Lemuroidea

DAUBENTONIIDAE

Daubentonia madagascariensis Gmelin

AYE-AYE

The aye-aye, which lives in Madagascar, has 1 young at a birth.

TARSIIDAE

Tarsius spectrum Pallas

SPECTRAL TARSIER

The Malayan tarsier is polyestrous and breeds all the year round with apparently little seasonal variation (1). The cycles average 23.5 ± 0.7 days. There is no bleeding from the vagina, and, at the time of heat, the vulva swells and the vaginal smear becomes entirely cornified. The stage of full cornification lasts for 24 hours and is followed by an invasion of leucocytes with recession of the vulva (2). Changes in the uterus have been described, but it is not clear to what stage of the cycle they belong. They consist of swelling of the glands, mitoses of the epithelial cells followed by localized congestion, and extravasation of blood, which is phagocytized and thus carried to the uterine cavity. There is no extensive desquamation of uterine epithelium (3).

1. Zuckerman, S. Proc. Zool. Soc., London, 1059–1075, 1933.
2. Catchpole, H. R., and J. F. Fulton. J. Mammalogy, 24: 90–93, 1943.
3. Herwerden, M. van. Monatsschr. f. Geb. u. Gyn., 24: 730–748, 1906.

LORISIDAE

Galago senegalensis Geoffroy

BUSH-BABY

The central African bush-baby appears to have a restricted breeding season lasting from December to July, with heat periods about 6 weeks apart. The distribution of births in the London Zoo also suggests a limited breeding season with December and January as its beginning (1). Heat lasts 5 to 6 days and is accompanied by a colorless discharge from the vulva. The usual number of young is 2, range 1 to 2. The period of gestation is 4 months. The female has a long, pendulous clitoris. The male reaches puberty at 20 months of age (2).

1. Zuckerman, S. Proc. Zool. Soc., London, 1059–1075, 1933.
2. Lowther, F. de L. Zoologica, 25: 433–462, 1940.

Other LORISIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Galago alleni Waterhouse	All year (Sanderson)			Nigeria and Cameroons
G. crassicaudatus Geoffroy Bush-baby	All pregnant early Sept. (Pitman)	1		Cent. Africa
Euoticus elegantulus Le Conte	No fixed season, appear to be breeding June–Oct. (Sanderson)			Niger and Congo River districts
Nycticebus malaianus Anderson			90 days	Malay Peninsula
N. tardigradus L. Slow Loris	Breeds all year, but may increase in fertility toward end of year (Zuckerman)	1	174–180 days	S.E. Asia

LEMURIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Hapalemur griseus Link		Dec.–Jan. (Schlegel)			Madagascar
Lemur macaco L. Lemur		Births in London Zoo nearly all March–June (Zuckerman)	1–2	146 days	Madagascar
L. mongoz L.			usually 1		Madagascar

LEMURIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
L. rubriventer Geoffroy			usually 2		Madagascar
Microcebus murinus Miller Gray Mouse Lemur	Pregnant Oct.–Nov. (Rand)		2–3, usually 2		Madagascar

INDRIIDAE

SPECIES	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Indri indri Gmelin Indri	1	60 days	Madagascar
Propithecus verreauxi Grandidier Sifaka	1		Madagascar

Anthropoidea

PLATYRRHINI

CALLITRICHIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Leontocebus rosalia L. Tamarin				140 days	S. America

CALLITRICHIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Oedipomidas geoffroyi Pucheran Squirrel Monkey	Feb. (Enders)	June	2		Cent. America

HAPALIDAE

Hapale jacchus L.

MARMOSET

Little is known of reproduction in the South American marmoset although it breeds readily in captivity. Puberty in the female occurs at 14 months of age, and the gestation period lasts 140 to 150 days (1). Combined data give the litter size as 1 to 3, with a mean value of 2.0 ± .04. The chorionic blood vessels anastomose, but no modification of the sex of twins has been observed (2).

1. Lucas, N. S., E. M. Hume, and H. H. Smith. Proc. Zool. Soc., London, 447–451, 1927.
2. Wislocki, G. B. Am. J. Anat., 64: 445–483, 1939.

CEBIDAE

Alouatta palliata Gray

HOWLER MONKEY

Not much is known of the reproduction of the howler monkeys of South America, but there appears to be no fixed breeding season (1). The ovarian wall thins during follicular enlargement, and a well-defined stigma is formed on the follicle. The theca interna is strongly marked. There is little luteiniza-

tion of granulosa cells in the ruptured follicle before the ingrowth of capillaries, but some luteinization of the interstitial tissue is already occurring. Fat is deposited in the cells of the theca interna and of the granulosa. The latter luteinize more slowly than the former, but eventually they are larger. The corpus luteum contains a cavity which disappears late in the lutein phase. The wall of the corpus luteum disappears so that this body becomes indistinguishable from the interstitial tissue (2).

The epithelium of the vagina keratinizes to a variable degree, and this change does not bear much relation to the stage of the cycle (2).

The endometrium during the follicular phase has low columnar epithelium with basal nuclei. The glands are straight, with many mitoses. In the luteal phase the epithelium is tall, the glands are coiled, and mitoses are frequent. Late in this phase there is marked degeneration and some desquamation of the endometrium. Red blood cells are extravasated, but these changes are not so intense as those which have been described for *Macaca* (2). The oviduct has a very narrow lumen as it passes through the uterine muscle. It has no sphincter, and no folds or villi (3).

The testes descend near the time of puberty (4).

1. Wislocki, G. B. Contrib. to Embryol., Carnegie Inst. of Washington, 414: 173–192, 1930.
2. Dempsey, E. W. Am. J. Anat., 64: 381–405, 1939.
3. Andersen, D. H. Am. J. Anat., 42: 255–305, 1928.
4. Wislocki, G. B. Human Biol., 8: 309–347, 1936.

Ateles geoffroyi Kuhl

SPIDER MONKEY

The South American spider monkey has no restricted breeding season (1), and the female menstruates periodically for 3 to 4 days at intervals of 24 to 27 days (2). The ovarian cycle is similar to that described for *Alouatta palliata*. In both species the corpus luteum becomes indistinguishable from the interstitial tissue in the lutein phase of the cycle (1,3).

The vaginal wall cornifies in the follicular stage, and a series of ridges and denticles develop. These, together with much of the cornified layer, are sloughed off late in this stage and for a short time after ovulation, but, though

the denticles disappear entirely, some cornified tissue is always present (3). The uterine changes resemble those described for *Alouatta palliata* (3).

The testes descend early in life, and the penis is covered with black, cornified barbs oriented backward from the head to the base of the penis, which may engage with the denticles which are present in the vagina of the female during the follicular phase. The clitoris is described as gigantic for primates, in which group it is usually small (4).

1. Wislocki, G. B. Contrib. to Embryol., Carnegie Inst. of Washington, 414: 173–192, 1930.
2. Goodman, L., and G. B. Wislocki. Anat. Rec., 61: 379–387, 1935.
3. Dempsey, E. W. Am. J. Anat., 64: 381–405, 1939.
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Cebus albifrons Humboldt

WHITE-FRONTED CAPUCHIN

The injection of 9,000 R.U. of estrogen in 11 days was not followed by menstruation upon cessation of the injections. During the injections epithelial cells in the vaginal smear increased in proportion to leucocytes, and after injections ceased the latter increased in numbers. Menstruation has not been observed in the normal female (1).

1. Zuckerman, S. J. Physiol., 84: 191–195, 1935.

Cebus apella L.

WEEPING CAPUCHIN

In the Ceylon Zoo this South American monkey copulates at night, usually at dusk, and the act is prolonged, lasting up to 20 minutes. There is no visible menstruation, and the period of gestation is 6 months (1).

1. Hill, W. C. O. Nature, 148: 408, 1941.

Cebus azarae Rengger

AZARA'S CAPUCHIN

The cycle of this South American monkey is from 16 to 20 days in length. Ovulation occurs about 9 days before the onset of menstruation. Copulation takes place at, or just before, the time of ovulation. Menstruation, which can be detected by the examination of vaginal lavages, is at the time of minimal vaginal desquamation, while at ovulation desquamation is maximal. The species breeds all year, but most births occur in May–June and October–November (1).

1. Hamlett, G. W. D. Anat. Rec., 73: 171–181, 1939.

Cebus fatuellus L.

BROWN CAPUCHIN

The injection of 3,500 R.U. of estrogen over a period of 13 days was not accompanied by, or followed by, menstruation. A few red blood cells were found in the lavage, but they are believed to have been due to trauma (1).

1. Zuckerman, S. J. Physiol., 84: 191–195, 1935.

Cebus vellerosus Geoffroy

THICK-FURRED CAPUCHIN

In the Ceylon Zoo this South American monkey, like *C. apella,* copulates at night, usually at dusk, and the act is prolonged, lasting up to 20 minutes. There is no visible menstruation and the period of gestation is 6 months (1).

1. Hill, W. C. O. Nature, 148: 408, 1941.

Other CEBIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	GESTATION PERIOD	HABITAT, ETC.
Alouatta seniculus L. Red Howler Monkey			139 days	S. America
Aotes zonalis Goldman Night Monkey	Possibly Dec. (Enders)	June		Cent. America
Ateles ater Cuvier Spider Monkey			139 days	Cent. America and northern S. America
Lagothrix humboldtii Geoffroy Woolly Monkey			139 days	Amazon, S. America
Saimiri oerstedi Reinhardt	Limited breeding season (Wislocki)			S. America. No sexual skin coloration, a small baculum

CATARRHINI

CERCOPITHECIDAE

Cercocebus torquatus Kerr

SOOTY MANGABEY

The sooty mangabey of West Africa has a menstrual cycle averaging 33.4 ± .1 days; range, 28 to 46; mode, 30 days (1). Swelling of the sexual skin subsides between days 14 and 20. Menstruation was not suppressed by the continued injection of estrogens unless they were started earlier than day 18 of the cycle (2).

1. Zuckerman, S. Proc. Zool. Soc., London, 315–329, 1937.
2. Zuckerman, S. Proc. Roy. Soc., London, 118B: 13–21, 1935.

Cercopithecus aethiops L.

GRIVET MONKEY

The African grivet monkey breeds all the year. Usually one young is born, twins are uncommon. The gestation period is about 7 months (1). There is no sexual skin or external swelling. Menstruation recurs at intervals of about 31 days. Injection of large amounts of estrogen into an ovariectomized female did not cause menstruation or withdrawal bleeding, and no external changes were observed (2).

1. Shortridge, G. C. The Mammals of South West Africa. London, 1934.
2. Zuckerman, S. J. Physiol., 84: 191–195, 1935.

Macaca irus Cuvier
(=*M. cynomolgus* Boddaert)

CRAB-EATING MACAQUE

The notes given here upon *Macaca irus* refer also to the similar species *M. fascicularis mordax* (1). According to Elliott, three separate species, *M. irus, M. fascicularis,* and *M. mordax* exist, but all are Malayan species and they are often included under the one specific name. There is no reason to believe that these forms differ in any details of their reproduction.

In a state of nature the crab-eating macaque appears to breed at any time of the year, but the peak of conceptions is in October and November (1,2). The cycle length is 25 to 29 days (1); 32.4 ± .5 days, mode 30, range 23 to 42 days (3); or 34.4 ± 1.6 days, range 24 to 52 days (4). The period of gestation is from 160 to 170 days (3). In the laboratory there tends to be an amenorrheic season in summer (4). The period of menstruation lasts from 2 to 13 days, usually 2 to 6 days. The color of the sexual skin intensifies (becomes redder) following menstruation, reaches its height at the mid-interval, and then diminishes (4). The time of greatest frequency of coitus occurs at 7 to 11 days after the beginning of menstruation (1).

The reproductive tract has been minutely compared with that of man. The labia minora are represented by fine membranous folds in the anterior

portion of the vulva, and the labia majora are often incomplete, especially the ventral portion. The vaginal epithelium is papillated and many lymph nodes are present. In the early interval the cells are stratified and cornified; later, denudation sets in. Most leucocytes are found just after ovulation. The time of greatest denudation is from 9 to 19 days, and of greatest leucocyte flow at 2 days and again 1 day before menstruation, at the time of the decline in the color of the sexual skin. The vaginal secretions are acid (1).

The cervical canal contains a pronounced fold, absent in man, which renders the passage tortuous. The uterine muscle contains a strong network of crossing fibers, absent in man, between the circular and longitudinal layers. At the myoendometrial boundary is a layer of cell islands. These are undifferentiated in the follicular phase, but at 12 to 14 days glycogen appears and the cells become flattened, so that the layer takes on the appearance of a muscularis mucosae. Dedifferentiation occurs at the end of the cycle. There are two main areas in which the blood vessels branch, the first at the level of these myoblasts, and the second near the surface of the mucosa. This second layer is mostly concerned in menstruation. Of the part of the endometrium which is shed at this time, two thirds is denuded early, and the last third after a slight interval. From days 5 to 14 regeneration occurs. The glands and blood vessels are straight at this time. From 8 to 14 days mitoses are common and the glands are sprouting. From 12 to 14 days the glands become tortuous, the capillary net is well developed, and plasma begins to flow into the stroma. From 15 to 18 days the glands are more tortuous, their epithelium is higher, and the nuclei are pressed to the bases of the cells while secretion begins. At 18 to 24 days mitoses have ceased, and the secretion gives glycogen and mucin reactions. Just before menstruation one finds hyperemia of the blood vessels and an outpouring of leucocytes. The vessels suddenly break down with loss of their epithelium, and blood pours into the stroma; denudation follows owing to the loosening of the tissues by the previous edema. All these changes closely correspond with those found in man (1).

In the ovariectomized female the injection of 250 to 1,000 R.U. of estrogen daily in increasing doses over a 12-day period (6,500 R.U. were injected in all) caused swelling of the sexual skin, and menstruation followed cessation of the injections (5).

1. Joachimowitz, R. Biol. Gen., 4: 447–540, 1928.
2. Herwerden, M. van. Tijdschr. Ned. dierk. Vereen., 10: 1–140, 1906.
3. Spiegel, A. Zent. f. Gyn., 22: 1762, 1931.

4. Corner, G. W. Anat. Rec., 52: 401–410, 1932.
5. Zuckerman, S. J. Physiol., 84: 191–195, 1935.

Macaca nemestrina L.

PIG-TAILED MACAQUE

Puberty in the female pig-tailed macaque is reached at about 50 months of age. The mean cycle length is 32.5 ± 1.5 days, the follicular phase lasting 14 days and the luteal phase 15 to 16 days (1). The sexual skin is well marked; it begins to swell during menstruation and regresses shortly before the middle of the cycle. The body weight increases in the first half of the cycle and begins to decline with the sexual skin. This seems to be due to the edema which is associated with the swelling. Less fluid is taken in during the swelling phase, but the urine output is much higher during the involutionary or luteal phase (2). The sexual skin responds to estrogens when it has been denervated (3). The red cell count in the blood is lowest at the beginning and end of the cycle, and highest at the middle (4). The period of gestation in one case was 171 days, and there was no menstruation or sexual skin swelling during lactation (5).

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2. Krohn, P. L., and S. Zuckerman. J. Physiol., 88: 369–387, 1937.
3. Zuckerman, S. Proc. Roy. Soc., London, 118B: 22–33, 1935.
4. Guthkelch, A. N., and S. Zuckerman. J. Physiol., 91: 269–278, 1937.
5. Zuckerman, S. Proc. Zool. Soc., London, 593–602, 1931.

Macaca radiata Geoffroy

BONNET MACAQUE

The bonnet monkey of southern India has a cycle length typical for the genus; four cycles ranged from 25 to 36 days and averaged at 29.5 days. The duration of gestation from the probable date of conception, in 3 cases, was 153, 166, and 169 days (1). The sexual skin is confined to the labia majora and the circumanal region, and is mostly an inconspicuous dark purple with

a little red at the margins of the labia and lateral streaks of red from the sitting pads and the tail base. There is a slight swelling of the area in the follicular stage (1).

The ovaries are more elongated than they are in the rhesus monkey. Interstitial tissue consists of a small amount of theca interna and abundant hyaline remains of atretic follicles. The cervix uteri is large and complex compared with that of the rhesus monkey, and it secretes much more mucus. Cyclical epithelial desquamation in the vagina is scanty (1). These facts greatly resemble those recorded for the related *M. pileatus,* which has not been treated separately.

Relaxation of the pelvic ligament as a preparation for parturition begins at about 5½ months (2). After ovariectomy the injection of 500 M.U. daily of estrogen induces a mucous flow, but there is little difference in the color of the sexual skin, which also changes but little during the cycle (3).

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2. Hartman, C. G., and W. L. Straus. Am. J. Obst. and Gyn., 37: 498–500, 1939.
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Macaca mulatta Zimmermann
(=*M. rhesus* Audebert)

BENGAL RHESUS MONKEY

In its native habitat the rhesus monkey is said to mate mainly in September and to give birth in March. This is in the Himalayas (1). In captivity the time of greatest fertility is from October to December, but breeding will take place at any time of the year. However, no conceptions have been recorded for June and July when menstruation is irregular or absent. There is also a lack of conceptions during the summer months in the Southern Hemisphere (2,3). The age at puberty is about 3 years, but reproduction is not regular until about 4½ years. Before this, menstruation may be irregular and it frequently occurs without ovulation (3). Puberty is reached gradually, with reddening of the buttocks as the first sign. This occurs, on the average, at 3,200 g. of weight, and the first menstruation at 3,600 g. (4), or 3,350 g. (range 3,040 to 3,850 g.) (3,5), but the average weight at first conception is 5,000 g. (3). The cycle length for a series from several labora-

tories gave a mode of 28 days; a mean of $27.36 \pm .17$ days, and a standard deviation of 5 to 7 days, with 75 per cent of cases falling between 23 and 33 days (3,4,6). The usual duration of menstruation is 4 to 6 days, with a spread from 2 to 11 days (6).

The time of ovulation, which is spontaneous (7), has been determined by rectal palpation. It varies from day 9 to day 20 of the cycle, with a pronounced mode at 13 days. The mean is also 13 days, and 77 per cent of ovulations fall from days 11 to 15 inclusive. However, in spite of its irregularity, the preovulatory interval is much more constant than the postovulatory period, suggesting that the corpus luteum has a variable length of life as compared with the period of growth of the follicle (8). This is not in agreement with the condition found in other species, but the data are reliable. Ovulation occurs from the right ovary in 50.8 per cent of the cases, which suggests that each sheds one egg with equal frequency. Lactation amenorrhea lasts, on the average, for 7 months (3).

The female permits coitus at any time in the cycle, but desire is greatest about 2 days before ovulation. No premenstrual rise has been observed (9), in contrast to the condition in man. The majority of conceptions occur between days 11 and 14, with a spread from day 9 to day 18 (3). Another record, which includes 160 pregnancies, gives the greatest fertility between noon of the eleventh and noon of the twelfth day of the cycle (10).

The number of young is usually 1; occasionally twins are born. The period of gestation in 29 cases ranged from 146 to 180 days, calculated from the probable date of ovulation. The mean was 163.7 ± 1.0 days, and the standard deviation, 8.0 days. The sex ratio of 36 births was exactly even (3).

HISTOLOGY OF THE FEMALE TRACT

OVARY. The corpus luteum of the cycle grows mainly by hypertrophy of the granulosa cells, with some growth by theca interna cells in the folds of the collapsed follicular wall. There is very little extravasation of blood at ovulation, and the fully formed corpus luteum is a solid structure with a prominence at the rupture point. Lipid degeneration of the cells occurs at the time of menstruation, and traces of the corpora persist for several cycles. The maximum size of the corpus luteum of the cycle is about 5.5 mm. in diameter (3,11). Three types have been described: the first is the normal one;

the second is a corpus luteum aberrens, which does not seem to produce progesterone and which contains large numbers of theca-lutein cells. This is a normal corpus luteum degenerating in an atypical manner. The third is similar but is derived from luteinized unruptured follicles (12). The nature and fate of the lipids in the cells have been carefully followed (13). The size of the ovum without the zona pellucida is 80 μ in diameter; with the zona it is 109 μ (3).

VAGINA. The vaginal epithelium has waves of growth and cornification which reach their height at the time of ovulation, and of desquamation, which is greatest just after ovulation (6). The vaginal lavage follows a similar curve with the greatest number of desquamated cells at the expected time, i.e., just after ovulation. Leucocyte counts fall near the mid-cycle and rise just before menstruation. On the whole the smear is not a good indication of the reproductive state, but the number of live leucocytes, i.e., those that resist the entrance of dye in a fresh lavage, appears to be significant (3). The cells of the vaginal wall are filled with glycogen (6).

UTERUS. The cervix uteri has several diverticuli in the canal and is more contorted than that of man. The line of transition between the cervical and vaginal epithelium is clear, but it varies in position in different animals (14). The uterine mucosa after the postmenstrual repair has a low surface epithelium; the gland tubules are straight and slightly dilated. Glycogen is most abundant in the cells at this time. In the lutein phase the glands become spiral and greatly dilated, and their epithelium is high, with roughened surfaces. The surface epithelium is high, the stroma becomes spongy, and mitoses are absent throughout the period. During menstruation blood is extravasated in the superficial layer of the endometrium, and the resulting hematoma lift off the epithelium and much of the mucous layer. Regeneration starts from the glandular epithelium (6).

Menstruation without ovulation has been described, and it appears to be especially frequent in adolescent monkeys. It occurs through the partial destruction of a preovulatory type of endometrium, and the usual premenstrual changes do not occur at all (15).

A few red blood cells may be found in the vaginal lavage at about ovulation time in many monkeys. Their appearance is much more frequent in winter, at the height of the breeding season, than in summer. Their origin does not seem to have been ascertained, and, in view of the occurrence of postestrous and proestrous bleedings in lower forms, further work might lead to results of interest (3).

Two types of arteries have been described in the endometrium. One type consists of longer arteries coiled for the entire height of the endometrium, with many elastic fibrils in their coats. The other type consists of smaller arteries which supply the pars basalis. They are devoid of elastic fibrils. The first types degenerates after ovariectomy but the second does not (16). The first type is involved in the breakdown which occurs in menstruation (17).

The cilia in the oviducts are active at all times during the cycle (6). Mitoses in the epithelium are most abundant at the time when the largest follicles are present in the ovaries, and they are most frequent at the ovarian end. Estrogen injections cause mitoses to appear in the tubal epithelium of ovariectomized females (18).

PHYSIOLOGY OF THE FEMALE TRACT

There is an evanescent swelling of the sexual skin in new-born monkeys of both sexes (19). This recalls the so-called genital crisis, or activity of the reproductive tract, which has been found in guinea pigs. It is believed to be due to the placental transmission of maternal hormones.

Bilateral ovariectomy at the beginning of menstruation is not followed by another period. If the operation is performed 72 hours or more after its beginning, or in the preovulatory phase, menstruation follows 5 to 6 days later even though the regular menstruation had not ceased at the time of the operation (20). These results are significant in relation to the occurrence of menstruation without ovulation. Ovariectomy in the postovulatory phase is also followed by bleeding (21). Hysterectomy has no effect upon the ovaries or on the cycle, as judged by vaginal desquamation or by sexual skin swelling (22,23).

In contrast to the results of ovariectomy, hypophysectomy early in the cycle is not followed by bleeding. If it is done in mid-cycle, when the sexual skin is well developed, bleeding follows after an interval of 2 to 4 days (24).

Abrupt changes in the color of the sexual skin do not occur during the cycle, but the color reaches its maximum intensity during the third week and diminishes before the end of the cycle. The swelling follows a similar series of changes (25). The skin is brilliantly colored during pregnancy. As the brilliance is known to be produced by the action of estrogens, this is to be expected (3).

The pH of the vaginal secretions of immature monkeys is 6.8 to 7.2. Under the influence of estrogen injections it fell to 5.5 to 6.0 (26). In mature ovariectomized females a fall from a level of 6.0 to 5.0 followed the injection of estrogens (27).

The erythrocyte count in the blood is lowest at the beginning and end of the cycle and highest at the middle. In the ovariectomized female it rises if estrogens are injected (28).

The excretion of estrogens in the urine of pregnant monkeys rises to a level of 75 to 450 I.U. per day by 60 to 110 days of pregnancy. It remains at a high level until a few days before parturition and then drops slightly. Androgens are excreted at a maximum level of 7 to 10 I.U. daily. The excretion of estrogens drops rapidly after parturition, but androgens continue to be excreted for a month (29).

Ovariectomy may be performed as early as the twenty-fifth day of pregnancy without causing abortion. The bright red color of the sexual skin is maintained throughout gestation and lactation, thus giving further proof that during pregnancy estrogens are secreted by tissues other than the ovaries (30).

The female is sexually very interested in the male at from 16 to 25 days of pregnancy (31). The placental sign, extravasation of blood from the uterus, which may be detected in the vaginal lavage, is first given at from 15 to 20 days, and it lasts 20 to 22 days (32). The pelvic ligament relaxes at 5½ months of pregnancy and is firm again within 3 to 4 weeks after parturition. These changes also occur in the ovariectomized pregnant monkey (33). Gonadotrophic hormones may be detected in the urine for a few days, i.e., from days 19 to 25, during pregnancy (34).

The activity of the oviducts during the cycle has been investigated. Spontaneous activity is lowest during the follicular phase. At ovulation the contraction rate is 8 to 13 per minute; it is not very regular and is rather undulatory in character. Contractions are slower during the lutein phase, but are more regular, with a rate of 3 to 8 per minute (35). The degree of spontaneous activity is said to be greatest at this time and during menstruation than it is in the follicular phase (36).

Progesterone in the blood has been found to be highest at days 10 to 11 of the cycle. It falls gradually during the lutein phase (37).

By calculating the minimal amount of estrogen needed to maintain the sexual skin in the ovariectomized female and to prevent the onset of menstruation, it has been deduced that the minimal daily output of estrogen

by the female macaque is 150 to 200 I.U. (38). The immature female requires 8 to 10 R.U. of estrogen daily to produce some reddening of the sexual skin, but 20 R.U. daily rising to 80 R.U. caused swelling as well as reddening. It took a week for the reddening to become appreciable, and by 22 days it was maximal. The epithelial cells in the vaginal smear increased and leucocytes decreased. The uterus grew, also the cilia in the oviducts, but the ovaries weighed less than normal (39,40).

In the mature ovariectomized macaque the injection of estrogens causes growth of the endometrium to the preovulatory stage. If they are given in threshold doses, i.e., from 75 to 150 I.U. daily, varying with the animal, and injections are continued at this level, bleeding occurs at intervals of from 5 to 8 weeks. Higher doses prevent the bleeding from occurring. It is believed, therefore, that the threshold of estrogen activity rises and falls in a rhythmic manner (41). These facts have given rise to the "estrogen withdrawal" theory of menstruation, which states that growth of the endometrium is due to the action of estrogen and that when the growth stimulus is removed degeneration sets in with consequent bleeding. The average dose that will build up the uterus to the stage where bleeding sets in after its cessation is about 125 I.U. daily for 10 days. The endometrium can be maintained after the building up by the daily injection of 50 to 100 I.U. of estrogen or by 0.5 mg. (= 0.5 I.U.) of progesterone (38,42). While 0.5 Rab.U. of progesterone will inhibit bleeding for a time, it will not do so indefinitely; for this to occur at least 1 Rab.U. is required (43).

The threshold single dose of estradiol benzoate which is followed by bleeding is 0.75 to 1.00 mg. However, in continued tests upon one animal the threshold appears to be lower if the initial dose is high and later injections are decreased, and higher if the initial injection is low and the threshold is reached by increasing the amount (44).

By use of the colchicine technic, which causes the accumulation of mitotic figures, the degree of sensitivity of various parts of the tract to estrogens has been worked out. Epithelial tissues are most sensitive, then stroma cells, and, lastly, muscle cells (45). The response of sexual skin to estrogens does not depend upon the nervous system, as denervated skin gives the usual reaction (46).

The bleeding which follows estrogen deprivation may also be prevented by the injection of testosterone propionate at the rate of 5 mg. daily. This amount will not prevent the bleeding which follows progesterone withdrawal, but 25 mg. daily has this effect (47). This amount injected into

normal females inhibits ovulation and menstruation and causes the clitoris to enlarge (48). The level of hormones required to produce progestational proliferation of the endometrium is 150 I.U. of estrogen daily together with 0.5 mg. of progesterone (43,49).

The ovaries of hypophysectomized monkeys will grow follicles if 50 I.U. of pregnant mares' serum is injected daily. If this is followed for 3 days by 100 I.U., they may be brought to the ovulation level (50). P.M.S. also appears to be the best substance at present available for causing ovulation in the summer anestrous period, but it is easy to produce overstimulation and luteinization. A dose of 200 I.U. daily has given the best results (51), but the time at which injections are made is important. The best time is from the sixth to eighth day of the cycle (52).

THE MALE

The male rhesus monkey does not have a sexual skin (53). He excretes 1.0 to 4.7 I.U. of androgens and 1.1 to 2.5 I.U. of estrogens each 24 hours (54).

In the presence of the testes or during the injection of testosterone the contractility of the vas deferens and seminal vesicles is inhibited, but the injection of estrogens stimulates them (55). The castrated adult requires the daily injection of 5 mg. of testosterone propionate to restore the sexual skin to its normal color (however, see above) and to produce normal accessory organs. When they are produced, they may be maintained with weekly injections of 17.5 mg. (56). In the hypophysectomized male 200 I.U. of P.M.S. gave some repair to spermatocytes. Given immediately after hypophysectomy, the same dose reduced the rate of degeneration of the testes, maintaining spermatogenesis for 20 days (50).

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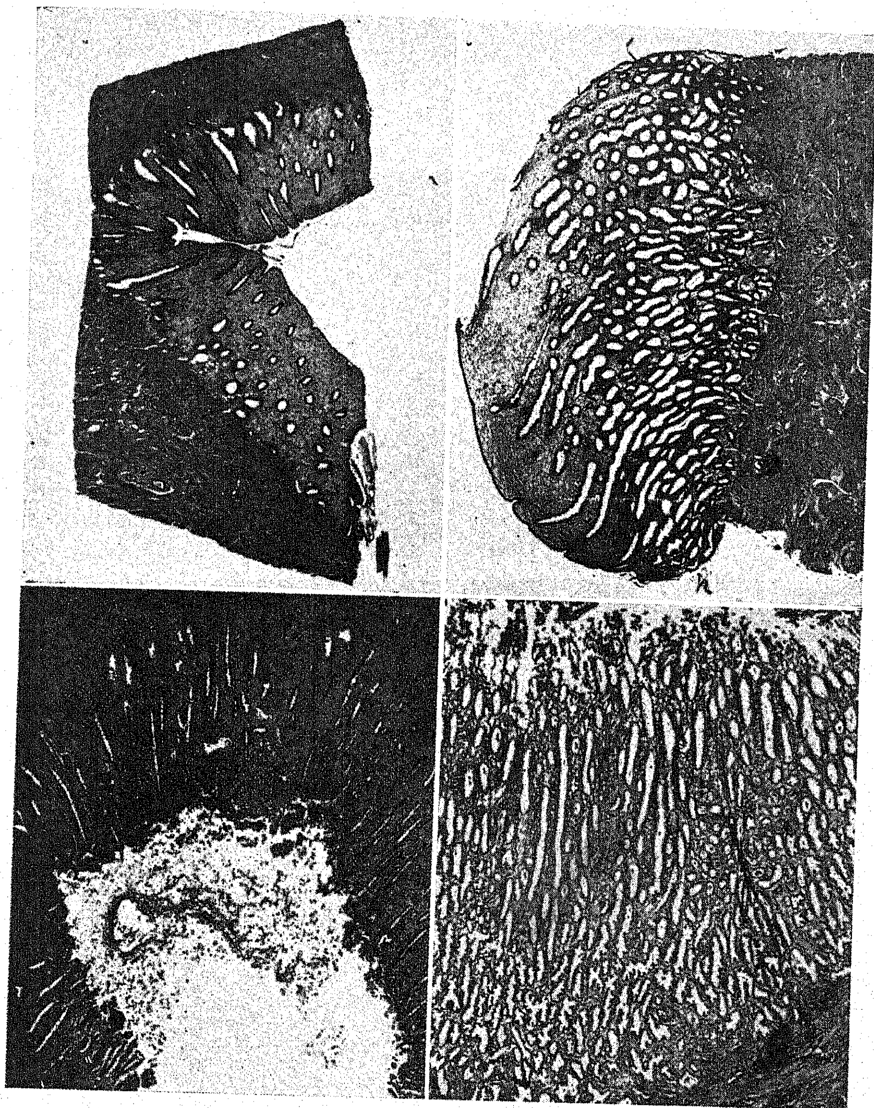

PLATE VII. Uterus of *Macaca mulatta,* changes in the cycle. *Upper left:* Proliferative endometrium. x13. (From G. W. Corner, Contrib. to Embryol., No. 75.) *Upper right:* Progestational endometrium. x13. (From G. W. Corner, Contrib. to Embryol., No. 75.) *Lower left:* Menstruation from proliferative endometrium, anovulatory cycle. x13. (From G. H. Daron, Am. J. Anat., 58: 349–419, 1936, by courtesy of Dr. G. W. Bartelmez.) *Lower right:* Menstruation from progestational endometrium, ovulatory cycle. x13. (From G. H. Daron, Am. J. Anat., 58: 349–419, 1936, by courtesy of Dr. G. W. Bartelmez.)

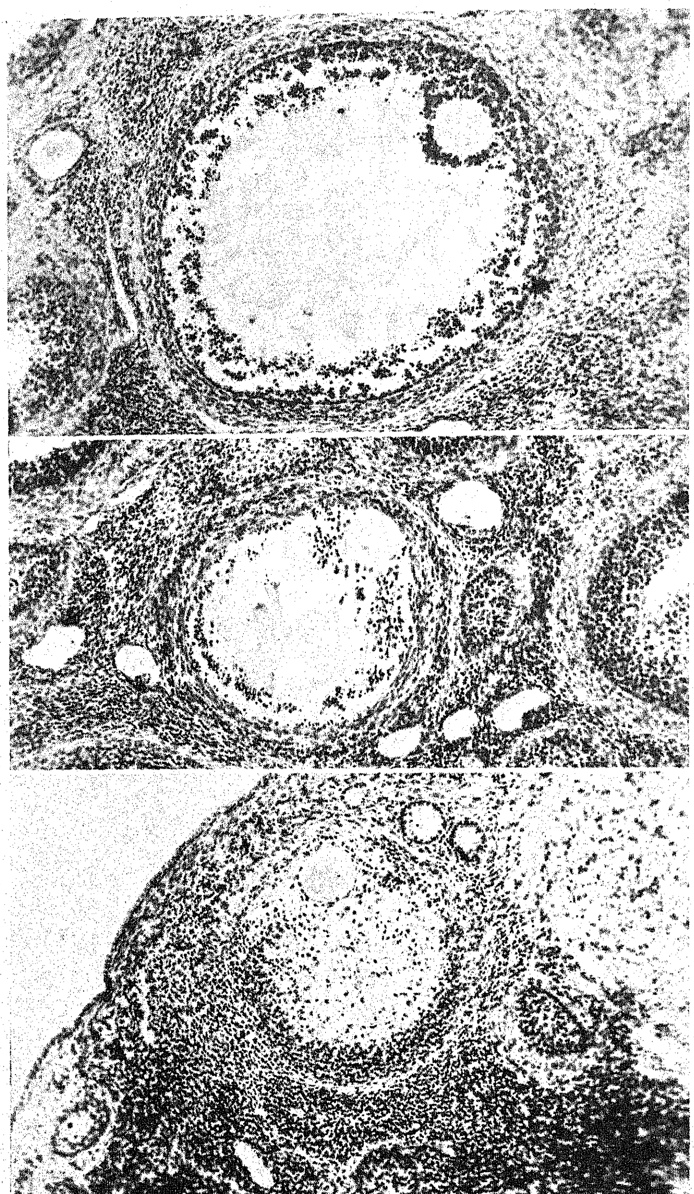

PLATE VIII. Follicular atresia, guinea pig. *Top:* Early stage. Note fragmentation of granulosa cells. H and E. x100. *Center:* Next stage. Note some disappearance of granulosa fragments and some growth of theca interna. H and E. x100. *Bottom:* Later stage. Note that the cavity is now filled with thecal cells. H and E. x100.

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Macaca sinica L.

TOQUE MACAQUE

The toque macaque of Ceylon has been treated here as a separate species from the bonnet macaque of Bengal, following modern usage.

The vagina is imperforate until puberty, which is reached at an age from 2½ to 3 years. At first, mucus is discharged, later bleeding sets in regularly in gradually increasing quantities. Puberty is accompanied by the reddening of some areas on the face. The sexual skin does not become edematous and it fades from bright purple to brownish after menstruation. There is a very large colliculus in the cervix uteri. The latter secretes large quantities of mucus during the cycle, which is usually 29 days in length. Menstruation lasts 1 to 4 days (1).

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Macaca sylvanus L.

BARBARY APE

The cycle of the Barbary ape is usually from 27 to 33 days, with menstruation lasting 3 to 4 days. The sexual skin is at a maximum at from 9 to 11 days and remains so for 4 days, after which regression is gradual. The vaginal

smear is not very informative, but just before menstruation it is caseous and richer in epithelial cells. The injection of 310 R.U. of estrogen daily into an immature female causes the sexual skin and uterus to develop. If this is followed by 24 Rab.U. daily of progesterone, the uterine glands develop to the premenstrual level (1). The gestation period is about 210 days.

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Papio cynocephalus Desmarest

YELLOW BABOON

The mean cycle length in two females of the yellow or Guinea baboon was 33.3 ± .7 days, the range was 25 to 41 days, and the mode was 31 to 32 days (1).

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Papio doguera Pucheran

DOGUERA BABOON

This baboon is probably the one described as *P. anubis*. If so, the following record is relevant. The mean length of 20 cycles was 34.7 ± .5 days, with a range of 28 to 38 days and a mode of 35 days. Menstruation is observed in this species (1).

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Papio hamadryas L.

SACRED BABOON

The sacred baboon breeds all the year round, but the height of the season is from May to July and the lowest point is in January and February (1).

The cycle is 31.4 ± .4 days (2) or 36.2 ± 1.5 days. Earlier cycles tend to be longer than those observed after the animals have settled down to laboratory life. The modal length of the cycle is 33 days in both series, and the follicular phase lasts 15 to 19 days. The duration of the lutein phase is 14 to 15 days (3). The number of young is usually 1, rarely 2 (4), and the period of gestation is about 183 days (5).

The reproductive tract is similar to that of *P. porcarius,* but the organs are smaller. The endometrium in the early lutein phase is 3.1 mm. deep, with high columnar epithelial cells which have granular cytoplasm and large, oval, vesicular nuclei, usually at the base of the cells. There is a good basement membrane; the glands are tortuous and are without the basal buds which have been described in man. The glands are barely secreting; there is no edema and few polymorphs. In the region of the isthmus the glands are shallower, wider, and mostly empty. At the end of menstruation the extravasated blood is localized, the glands straight, long, and thin, with little secretion. There are numerous leucocytes and also a good basal membrane. In the follicular phase the endometrium is 3.8 mm. thick. The free edge of the columnar epithelium is covered by a thin layer of secretion. The nuclei are large with numerous mitoses. The glands are simple, straight tubules, few in number and with little secretion. Numerous mitoses and many wandering cells are present. The stroma is open, with numerous mitoses and many leucocytes (2).

Ovariectomy causes an immediate reduction of the color of the sexual skin below the resting level. From 60,000 to 80,000 M.U. of estrogen are needed to cause complete swelling of this area (6).

After castration the male loses its cape of gray fur and the sexual skin regresses, both on the snout and on the buttocks. The injection of testosterone at the rate of 100 mg. per week restored all these features. The snout began to color in 2 weeks, the buttocks were enlarged and began to color in 1 month, and the cape was restored in 5 months (7).

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Papio leucophaeus Cuvier

DRILL

The drill has a menstrual cycle of $32.6 \pm .9$ days (1). The injection into an immature male of 50 mg. of testosterone twice weekly, working up to 300 mg. weekly, caused the premature development of secondary sexual characters. Within a week the circumanal region of red extended and became more intense; this condition was followed by swelling. At the end of the first month the face began to change color, and, by the third month, it resembled that of an adult male. In three months the scrotum began to color. Removal of one testis proved the immaturity, and when the injections were stopped the colors faded and the swelling subsided (2).

1. Zuckerman, S. Proc. Zool. Soc., London, 315–329, 1937.
2. Zuckerman, S., and A. S. Parkes. J. Endocrinol., 1: 430–439, 1939.

Papio porcarius Brunnich (=*P. comatus* Geoffroy)

CHACMA BABOON

The Chacma baboon of South Africa breeds at any time of the year (1). Puberty is probably reached at about 4 years of age (2). The cycle is irregular in its length, but the external changes, i.e., swelling of the perineal region and vaginal discharge, are much more pronounced than they are in most monkeys. A record of 9 cycles in one female gave a range from 34 to 67 days, with an average of 41 days (3); another series of 4 ranged from 30 to 39 days, average 35 days (4); a series of over 20 cycles in different baboons ranged from 29 to 63 days, average 42 days (5). The modal point is difficult to determine with such a large spread, but it appears to be about 34 to 36 days. However, the figures include many winter cycles when the length tends to be much greater than it is during the fall (5). One, rarely two, young are born at a time, and the period of gestation is about 7 months (6). There is no ovarian activity during lactation (7).

The area of external swelling extends from the root of the tail to a curved line drawn through the junction of the abdominal wall with the front of the thighs. The changes in this area may be divided into three periods: perineal rest, perineal turgescence, and perineal deturgescence. The period of perineal rest begins 1 to 5 days before menstruation and continues through menstruation and afterwards for 7 to 25 days. The period of turgescence lasts from 11 to 19, usually for 16 days. There is a sudden diminution in the degree of swelling 24 hours before the maximum is reached, then a sudden great increase which lasts 1 day. It is believed that the sudden fall coincides with ovulation. Perineal deturgescence is usually rapid, but may last from 4 to 18 days, and shows great variability. In winter turgescence lasts a shorter time, and the rest period is longer, than at other times of the year. The degree of swelling is greatest in April and May, i.e., during the fall. At the beginning of turgescence a thick white discharge oozes from the vagina. This becomes thicker until maximum turgescence is reached, and at this time it forms a false vaginal plug. About 8 days before the onset of menstruation the secretion becomes scanty, thin, and clear (5).

Menstruation lasts overtly for 4 to 9 days, though red blood cells may be detected microscopically in the vaginal lavage for 4 to 19 days, but usually for 9 days (5).

The changes in the internal organs have been well worked out and they are described as resembling those found in *P. hamadryas*. The size of the resting follicle is about 1 mm. in diameter, and of the mature follicle, 6.3 mm. There is a wave of growth at the beginning of the follicular phase, but it is not necessarily the largest follicle which ovulates. No conelike extrusion forms on the follicle which is destined to rupture. At ovulation some blood is extravasated, and it remains mostly at the periphery of the developing corpus luteum. After rupture the follicle shrinks to 4 mm., and all its layers are much folded over so that the developing corpus luteum is lobulated. Full development is reached very slowly, and theca cells do not share in the luteinization. During menstruation the cells of the corpus luteum become vacuolated, and connective tissue increases enormously. The lutein cells measure 11.8 μ at their maximal development, which is reached after 7 days in the corpus luteum of the cycle. The maximal size of the corpus luteum during pregnancy is 6.7 mm., with the cells averaging 21.2 μ. There is no evidence for waves of follicular growth and atresia during pregnancy. The corpus luteum persists throughout this period but disappears rapidly after

parturition. Hyaline atresia of follicles is found but is not so frequent as in *Macaca irus* (8).

Growth and keratinization of the stratified vaginal epithelium begins during menstruation. It continues throughout the follicular phase and produces a characteristic corrugation of the epithelium. Cornification is intensified at ovulation, and there is considerable sloughing after it. At this time leucocytes are scarce, but they increase throughout the luteal phase (8).

During the luteal phase the endometrium is 5.4 mm. thick. The epithelium is high columnar, with oval vesicular nuclei. Few leucocytes are present. The glands are very coiled, with numerous basal buds, and they secrete during the mid-luteal phase. The stroma is edematous in its middle zone. At menstruation about two thirds of the endometrium is sloughed off (8).

The cervix is coated with stratified epithelium for 3 to 4 mm. from the os uteri, then there is an abrupt change to columnar epithelium, with glands which enlarge enormously during pregnancy. There is little morphological change during the cycle, but much secretion occurs in the mid-luteal period (8).

The medial third of the oviduct is straight and the rest is coiled. The fimbriated end is large and deep red. The oviduct as a whole increases in vascularity immediately after ovulation (8).

If progesterone is injected in the first half of the cycle, deturgescence results and menstrual bleeding may occur. The minimal dose for deturgescence is 3 mg., and for bleeding, 20 mg. in a single dose, or 15 mg. if it is given in 5 mg. doses at 3 to 4 days apart (9). Deturgescence is also caused by the injection of estradiol benzoate early in the cycle; 0.1 mg. produces slight deturgescence, but with 1.0 mg. it is complete. As the cycles were lengthened, it is believed that the effect is produced by an action upon the ovaries (10). In the spayed baboon the minimal daily dose for 15 days sufficient to produce slight turgescence was 0.01 mg. of estradiol benzoate. Daily injections of 0.02 to 0.04 mg., usually 0.04 mg., produced an effect similar to that found in the normal baboon. The daily dose needed to build the endometrium to a state in which bleeding followed the cessation of injections was .01 to .06 mg., usually 0.01 to 0.02 mg. (11).

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Presbytis entellus Dufresne

LANGUR

Not much has yet been learned of reproduction in the Indian langur. Menstruation is said to occur each month and to last about 4 days. Extravasation of blood begins on the dorsal side of the uterus. The epithelium of the cervix is not cast off during menstruation, and the glands in this region actively secrete during this time. In general, the uterine changes recall those found in the macaque. Ovulation probably occurs in the interval, but menstruation may happen without it (1).

The langur not infrequently has twins (2). An immature male was injected with testosterone twice weekly. By 4 weeks the glans protruded from the penis, and the sexual skin reddened and became enlarged (3).

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Other CERCOPITHECIDAE

SPECIES	BREEDING SEASON	GESTATION PERIOD	HABITAT, ETC.
Cercocebus albigena Gray Gray-cheeked Mangabey	Cycle length 29 days av. menstruates, sexual skin swells (Zuckerman)		Congo

Other CERCOPITHECIDAE (*Continued*)

SPECIES	BREEDING SEASON	GESTATION PERIOD	HABITAT, ETC.
Cercopithecus cynosura Scopoli Guenon		7 months	W. Africa
C. mitis Wolf Pluto Monkey	Cycle length 30 days(?). Menstruates (Zuckerman)		Cent. Africa
Macaca maurus Cuvier Moor Macaque	30–40 days cycle (Zuckerman)		Celebes. Striking sexual skin changes
Papio sphinx L.		220 days	
Mandrill		270 days	
Presbytis priamus Blyth Madras Langur		196 days	India

HYLOBATIDAE

Hylobates hainanus Thomas

HAINAN GIBBON

The Hainan gibbon, according to the observation of one specimen, reaches puberty at about 7 years of age. Menstruation recurs at intervals of a little over a month and it lasts about 2 to 3 days (1).

1. Pocock, R. I. Proc. Zool. Soc., London, 169–180, 1905(2).

Hylobates lar L.

GIBBON

The average length of 17 cycles in two adult females of the gibbon was 29.8 ± .6 days, with a range from 21 to 43 days. Bleeding lasted 2 to 5 days, averaging 2.4 days. There is no sexual skin swelling, but the labia vary in their degree of extrusion and coloring (1). Puberty is probably reached at the age of 8 to 10 years, and there is no regular breeding season (2). One young is born at a time.

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Hylobates hoolock Harlan

WHITE-BROWED GIBBON

The white-browed gibbon of India has 1 young at a birth.

PONGIDAE

Pan satyrus L.

CHIMPANZEE

The chimpanzee breeds all the year round. Puberty is gradual with swelling of the sexual skin as the first sign of its approach. This may last for some months, and then the swelling subsides, upon which menstruation follows in a few days (1). The mean age at first menstruation (menarche) is 8 years 11 months. The young females are not immediately fertile, and they may not become pregnant for from 4 months to 2 years, with a usual interval of

from 1 to 1½ years. The mean cycle length during the first few months is 50 ± 4.4 days; later, when the females are fully adult, the mean length becomes 34 to 35 days, which may be taken as the true mean cycle length. In adolescents, during winter, there is a tendency to a prolonged preswelling stage with amenorrhea. Isolation, copulation, and the sex of the cage mate have no effect upon the cycle length. The most constant parts of the cycle are the postswelling stage and menstruation. The latter lasts about 4 days in adolescents and 2 to 3 days in adults (2). The spread is from 1 to 7 days (3).

The sexual skin does not show such marked color changes as those observed in macaques, but the swelling is very great, amounting in some cases to an increase of 1,400 cc. in volume. It is caused by the accumulation of intercellular fluid. For several days after menstruation the sexual skin area is quiescent, then swelling begins, the time depending upon the length of the cycle. At first the labial and circumanal regions are involved, then it spreads anteriorly through the prepudendal region and laterally to the callosities. Usually the maximal swelling is reached at about the fifteenth day of the cycle, and it subsides about 11 days before menstruation begins, but there is often a partial renewal a day before menstruation. Detumescence is rapid, occupying about 48 hours (3). The two periods of maximal swelling coincide with, or just precede, the periods of greatest estrogen excretion in the urine.

Ovulation occurs usually from the sixteenth day of the cycle onward, as judged by the dates of fertile matings, but it is believed that a more accurate dating can be made by referring it to the probable date of the next menstruation. By this method it is believed to occur about 14 days before the next missed period, a time which is in close agreement with that in macaques and man (4). A definite rhythm of sexual receptivity has been observed. This is zero during menstruation and in the immediate postmenstrual period. Maximal receptivity occurs between the middle and the end of the time of maximal swelling, then it falls to zero and remains so for the rest of the cycle, i.e., it falls abruptly at days 18 to 22 (5).

The vaginal smear changes somewhat during the cycle. The number of epithelial cells falls just before menstruation and increases early in the lutein phase. Leucocytes are very variable (6). A vaginal plug is formed after copulation (7).

The number of young born is usually 1; occasionally there are twins; and the mean duration of gestation is 236.5 ± 2.1 days from the probable date of conception. The range is from 216 to 261 days, and the standard deviation is 13.3 days (8).

The excretion of estrogens in the urine amounts, at its maximum, to 200 to 400 I.U. per 24-hour sample. The peak is reached at the time of maximal genital swelling and just before menstruation. The excretion of androgens is about 4 to 8 I.U. daily, and it is subject to irregular variation. Males excrete about twice as much androgen and somewhat less than half as much estrogen as females (9,10).

The injection of 3,000 R.U. of estrogen over 3 days into an immature ovariectomized female caused sexual skin swelling to begin. It reached its maximum by 15 days, when 16,000 R.U. had been given (11).

The Aschheim-Zondek urine reaction for the diagnosis of pregnancy is given by the chimpanzee, but it appears to be usable only for a limited period toward the beginning of pregnancy (12). This reaction depends upon the excretion of gonadotrophic hormones.

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Other PONGIDAE

SPECIES	BREEDING SEASON	GESTATION PERIOD	HABITAT, ETC.
Gorilla gorilla Wyman Gorilla	Cycles about 45 days (Nobach)		Cent. Africa
Pongo pygmaeus Hoppius Orang-utan	Cycles about 29 days (Zuckerman). Sexual skin swelling restricted to pregnancy (Schultz)	8–9 months	Malay Archipelago

HOMINIDAE

Homo sapiens L.

MAN

The literature relating to reproduction in man has not been covered as thoroughly as that relating to other species since many excellent books are available dealing with the subject. In this review a few points have been emphasized in order to illustrate the essential similarity between human reproduction and that of other species. Experimental difficulties limit the amount of knowledge on many points which have been worked out in other mammals.

The mean age at the menarche for about 115,000 cases, mostly of whites in many countries, is 15.45 ± .004 years; standard deviation, 2.15; and mode, 14.5 years. It is generally held that it is earlier in races living in warm climates than in those inhabiting colder ones. The evidence hardly supports this view, and doubtless other factors, especially that of nutrition, modify the data, which have been summarized in graphic form (1,2). The menarche occurs much less frequently in summer than in winter in New York (3). The human subject probably frequently experiences menstrual periods without ovulation in the earlier years of reproductive life, and a few such cases have been recorded (4).

Accurately recorded cycle lengths are few and far between, and the variability is greater than is usually realized. Material gathered from several sources gave, after abnormally long cycles had been eliminated, following our practice with other mammals, a mean length of 28.32 ± 0.6 days, a standard deviation of 5.41 days, and a modal length of 27 to 28 days. Eighty per cent of the cycles lay between 21 and 34 days. These figures are very close to similar ones calculated for the rhesus monkey; the mean length is one day more in man. The duration of menstruation normally varies from 2 to 8 days, with a mode at 5 days (5).

The time of ovulation in relation to the cycle has occasioned much controversy. Several lines of evidence agree in dating it near the middle, counting from the first day of menstruation (6). According to some workers (7) it occurs invariably 15 days before menstruation, but most are unwilling to

agree that it is so definitely fixed. It would constitute a most unusual biological phenomenon if there were not some variation. Attempts have been made to solve the problem by plotting the times at which a single coitus within the cycle must have been the cause of a pregnancy (8). These have shown that conception may result at any time but that it is most likely in mid-cycle. Work of this nature is open to the criticism that it depends upon statements which may be unreliable. Biologically it is only an approximation because the data are plotted on a standard 28-day cycle which is merely the average duration. The data cannot be plotted exactly since the fact that pregnancy has ensued interrupts the cycle.

A phenomenon which, so far, has only definitely been found in man is the menopause, or cessation of ovarian function, at a fairly definite time of life. This is a very gradual process, as, toward the end of reproductive life, the cycles become more irregular. The modal age at the menopause has been given at 49 years (1). The ovaries become less responsive to gonadotrophic hormones at this time, and the amount of follicular atrophy increases together with the amount of connective tissue. The amount of F.S.H. in the anterior pituitary increases and a gonadotrophe consisting almost entirely of F.S.H., or its equivalent, appears in the urine. These changes in the activity of the pituitary and excretion of F.S.H. are also found in ovariectomized women soon after the operation (9). Probably, if we had more information upon the latter part of life in other primates, similar findings would be recorded for them. The cessation of reproduction in rats is a much more gradual process, some ceasing early and others continuing to be in good reproductive condition to the end of a very long life. They do not show a cessation of reproduction at a fairly definite age as does man.

Fecundity has been thoroughly studied, and the results may be found in books on population statistics. Twinning usually occurs once in about 83 births; triplets are said to occur once in 83^2 and higher numbers in increasing powers, an approximation which gives a good idea of their frequency. Hospital records suggest that twinning is more frequent in East Indians and in Negroes than it is in whites (10), but the data may be biased as it is probable that hospitalization is more frequent among colored races when birth difficulties are anticipated. This illustrates the difficulty encountered in assessing the value of any human statistics in which complete registration is not the rule. Identical twins, or those which arise from one fertilized egg (monozygotic twins), are frequent, accounting for 25 per cent of all twins born. The sex ratio for a very large body of statistics is 51.05 per cent males. Racial

and national differences have been observed, but it is not clear how far these are due to imperfections of registration.

The duration of gestation is usually calculated from the first day of the last menses. One set of data calculated in this way gave 280.2 ± .3 days, standard deviation 9.2 days. Another set calculated from the last day of the last menses gave 274.0 ± .3 days, standard deviation 10.4 days. When allowance is made for the duration of menstruation, these averages are in close agreement. If the average date of ovulation is 13 days from the last menses, the average actual duration of gestation is 267 days. The duration of gestation in man is more variable than it is in any other species with available records (11).

The histology of the tract of women is similar to that of the rhesus and the crab-eating monkey (*Macaca*), and the changes during the cycle are essentially the same. As accurately dated nonpathological material is scanty, the literature is not reviewed here. The tubo-uterine junction is not guarded by folds of mucosa (12). Air can be forced from the uterus into the tube at a pressure of about 100 mm. mercury, but, when the flow is established, the pressure falls to 40 mm. (9). The vaginal smear can be used with care for distinguishing the phases of the cycle, but the changes are not clear-cut. The percentage of cornified cells rises sharply at about the time of ovulation, and there is some indication that it does so also just before menstruation in ovulatory cycles. Leucocytes are more abundant just after ovulation. The amount of desquamation is less in man than it is in the rhesus monkey (13,14).

The pH of the vaginal secretions varies from 4.0 to 5.0 depending upon the stage of the cycle. The highest degree of acidity is found in mid-cycle, at about the time of ovulation (15). The reaction in man is considerably more acid than that found in any other species, including the macaque, in which it is also somewhat unusually acid.

Work on the motility of uterine muscle has yielded somewhat conflicting results, but what is known seems to be generally in line with the findings in other species. In general, contractions are rapid and regular during the follicular phase of the cycle, less rapid and more irregular, but stronger, in the lutein phase, with an increase in irritability just before and at menstruation (9). Recently, the results (7) which indicate that after ovulation, i.e., during the lutein phase, the myometrium loses its reactivity to pituitrin, have been challenged (9).

Contractions of the oviduct during the mid and late interval are rapid

and variable in height, while in the premenstrual and menstrual phases they are slower and more uniform in amplitude (16). At mid-interval the epithelial cells are tall columnar, and, just before menstruation, they become cubical and irregular. There seems to be no cyclical variation in the number or height of the cilia (17).

Estrogens may be detected in the blood and urine during the cycle in varying amounts. A peak in excretion, about 1,000 I.U. in 24 hours, occurs at about the mid-interval, near ovulation time (18). Some workers have found a second peak a few days before the onset of menstruation. In pregnancy the usual pattern of excretion is followed. It is low for the first 8 weeks, 200 to 1,000 I.U. daily; and it rises steadily to term, when 15,000 to 40,000 I.U. are excreted each day (19). Corresponding changes have been observed in the level of estrogens in the blood.

Progesterone is excreted in the urine as pregnandiol, a compound which has only been found elsewhere in the urine of the chimpanzee. Naturally it is only found when a corpus luteum is present in the ovary. Its excretion begins about the mid-interval, reaches a peak in a few days, and disappears rather abruptly from 1 to 3 days before menstruation (20). It is also present during pregnancy, but it is not excreted in greater amounts than it is in the luteal phase of the cycle until the sixty-ninth day. It then rises steadily until delivery, when the amount excreted falls abruptly (21).

Gonadotrophic hormones have been found in the blood and urine of the newborn, and they are believed to have originated in the mother and to have crossed the placenta. Their appearance is brief and inconstant and may be related to the "genital crisis," or brief uterine hemorrhage, found in some newborn babies (9). They reappear in appreciable quantities at the menarche and have been observed to fluctuate with the cycle, the amount reaching a peak in the mid-interval, but the individual variation is great. It has been stated that F.S.H. activity is more apparent in preovulatory blood than it is later. During pregnancy the amount of gonadotrophic hormone in the urine, principally L.H. in type, rises rapidly from about the time of the first missed period to the sixtieth day. Then it gradually declines, but the amount is still appreciable at parturition (9). The human female differs from other species in this respect. Such gonadotrophins are found for a limited time in the urine of the pregnant chimpanzee, and, for a still more limited period, in that of the pregnant macaque. Other species which have been tested, except the giraffe, have given negative results. The hormone is believed to be of placental origin. A gonadotrophic substance, almost purely

F.S.H. in its activity, is also found in the urine for a variable time after ovariectomy and after the menopause. Possibly its appearance is related to the increased F.S.H. content of the anterior pituitary under these conditions.

The anterior pituitary of the normal human is exceptionally high in F.S.H., and low in L.H. The male pituitary has about half the activity of the female for both these hormones (22). Data on lactogenic activity appear to be wanting.

The amount of estrogen needed to build the endometrium of the ovariectomized woman to the point at which bleeding follows cessation of the injections is 1.5 to 2.0 mg. of estradiol benzoate weekly (23), or 4,200 I.U. daily. The amount of progesterone secreted by the corpus luteum may be estimated by the amount of pregnandiol excreted. If this is a reliable indication, and methods of assay are not yet very accurate, the corpus luteum of the cycle secretes between 5 and 20 mg. daily (4). At the third month of pregnancy the amount is about to 10 to 20 mg. daily (23). It is not certain, however, that all of this substance is produced by the corpus luteum; the fact that pregnancy may be continued after ovariectomy as early as the second month is an indication of possible secretion by another organ, probably the placenta.

THE MALE

The normal ejaculate of the male is about 3 to 5 cc., containing 100,000,000 to 150,000,000 spermatozoa per cc. (24). The pH varies from 6.9 to 7.36, with an average of 7.19. Prostate fluid ranges from 6.3 to 6.6, average 6.45, and that of the seminal vesicles averages 7.29 (25). Human semen is exceptionally well buffered (26), which may explain why the spermatozoa are able to survive the exceptionally acid reaction of the vagina. It is liquid when it is ejaculated and rapidly coagulates, but liquefies in a few minutes. The prostatic fluid is rich in an enzyme, fibrinolysin, which liquefies fibrin (27,28). Prostatic fluid is high in Na, K, and Ca, and that of the seminal vesicles is high in acid-soluble phosphate (25).

Androgen excretion in the urine averages 13.8 mg. daily, but the range is considerable, being from 8.1 to 22.6 mg. Excretion of these substances does not follow a cyclical pattern. The castrate excretes about half the amount of androgen excreted by the normal male, and, in normals, the amount decreases with advancing age (29). Normal females excrete about

the same quantities of androgens as do normal males; and the male excretes estrogens, but without cyclical variation (9).

Spermatozoa take 19 to 23 days for their passage through the epididymis (30). Their length of life in the female tract is for a limited time only, but reports of maximum survival vary from 2 to 5 days. The vagina is the least healthy environment for them and the cervix the best (9).

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5. King, J. L. Contrib. to Embryol., Carnegie Inst. of Washington, 363: 79–94, 1926.
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18. D'Amour, F. E. J. Clin. Endocrinol., 3: 41–48, 1943.
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CARNIVORA

THE patterns of reproduction in Carnivora vary widely in the different families. The Ursidae appear to be monestrous, the young are born in a very immature state, and delayed implantation of the blastocysts is suspected. The Mustelidae have a restricted breeding season in which waves of follicles ripen. Induced ovulation is definitely the rule in two species, and it probably occurs in others. Some species have an excessively long gestation period, almost a year, and in these delayed implantation is the cause. The latent period may be shortened by exposure to greater amounts of daylight. Most Canidae are monestrous, and they have a prolonged pseudopregnancy in the absence of pregnancy. Extravasation of blood in the uterus seems to be the exception rather than the rule. It has been found definitely only in the genus *Canis*. The Felidae appear to be seasonally polyestrous in temperate regions and completely polyestrous in the tropics, though our knowledge of the smaller tropical species is inadequate for generalization. Probably induced ovulation is the rule in many species of this family.

URSIDAE

Euarctos americanus Pallas

BLACK BEAR

The black bear of North America mates in June or early July. Implantation is probably in November, and the young are born, very immature, late in January and early in February. The time of ovulation is not known; hence, instead of delayed implantation, this may be a case of delayed ovula-

tion (1). Puberty is reached at about 3 years of age, gestation from the time of coitus is about 7 months, and the number of young born is 1 to 4, but usually 2 to 3 (2).

1. Hamlett, G. W. D. Quart. Rev. Biol., 10: 432–447, 1935.
2. Grinnell, J., J. S. Dixon, and J. M. Linsdale. Fur Bearing Mammals of California. Berkeley, 1937.

Ursus arctos L.

EUROPEAN BROWN BEAR

The common brown bear of the Old World reaches puberty at 6 years and remains fertile until its thirtieth year. Mating is in April–June, and the period of gestation is about 7 months (1). The young are born from December to January, depending on the locality, and it is believed that delayed implantation is the rule (2). In the Himalayas the mating season is said to be from the end of September to November, and the young, usually 2, or 1 with young females, are born in April or May (3).

1. Popoff, N. Compt. Rend. Assn. Anat., 29: 471–484, 1934.
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Other URSIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Melursus ursinus Shaw Indian Sloth Bear	June (Blanford)	Oct.–Feb., usually Dec.–Jan.	2	7 months	India
Selenarctos ussuricus Heude Manchurian Black Bear			2		Born in hibernation (Sowerby)
Thalarctos maritimus Phipps Polar Bear	Feb.–March	Dec.–March		8 months in captivity	Probably delayed implantation (Hamlett)

Other URSIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Ursus horribilis Ord Grizzly Bear	June–July	Jan.	1–4, usually 2	6–7½ months	N. America. Probably delayed implantation (Hamlett)
U. klamathensis Merriam Klamath Grizzly Bear		Jan.–Mar. (N.A.F. 55)	2–4		Oregon and California
U. torquatus Wagner Himalayan Brown Bear		Spring (Blanford)	usually 2		Himalayas

AILUROPODIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	HABITAT, ETC.
Ailuropoda melanoleuca Milne-Edwards Giant Panda	Early spring (Sheldon)	Jan.	China

PROCYONIDAE

Procyon lotor L.

RACCOON

The female raccoon breeds at 1 year of age, and the breeding season is from the first week in February to the first week in March, though there may be another heat later in the season (1). In New England mating begins in the last week of January and there may be a later season for young females, as some are born in August (2). The female is receptive at 1 to 2 weeks after the onset of vulval swelling and she remains in heat for 3 days. The average

gestation period is 63 days. The testes reach their full size in the fall of the second year, and the male is capable of mating at any time (1). The female possesses an os clitoritidis (3). The litter size is $3.5 \pm .15$, with a range from 1 to 6, and a mode of 3 to 4 (4). If raccoons are exposed to an increased length of light in the fall, they will breed in December and may be induced to produce two litters a year (4).

1. Stuewer, F. W. J. Wildlife Management, 7: 60–73, 1943.
2. Whitney, L. F. J. Mammalogy, 12: 29–38, 1931.
3. Rinker, G. C. J. Mammalogy, 25: 91–92, 1944.
4. Bissonnette, T. H., and A. G. Csech. Proc. Roy. Soc., London, 122B: 246–254, 1937.

Other PROCYONIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Aelurus fulgens Cuvier Himalayan Raccoon		Spring (Blanford)	2		S.E. Himilayas
Nasua nasua L. Coati			4–5	77 days	S. America. Two records (Enders)
Potos flavus Schreber Kinkajou	April		1		Cent. and S. America. One record
Procyon psora Gray Raccoon				65 days	Western U.S.

BASSARISCIDAE

SPECIES	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Bassariscus astutus Lichtenstein Ring-tailed Cat	May–June	3–4	Western N. America

MUSTELIDAE

Lutra canadensis Schreber

CANADA OTTER

The North American otter reaches sexual maturity at the age of 1 year. Mating is in February (1), and the young are born in April in the north, but earlier toward the south of its range (2). There is one litter a year of 1 to 4, usually 3 to 4 (3), and the gestation period is about 2 months (1).

1. Am. Fur Breeder, 14(6): 36, 1941.
2. Bailey, V. North American Fauna, No. 55, 1936.
3. Grinnell, J., J. S. Dixon, and J. M. Linsdale. Fur Bearing Mammals of California. Berkeley, 1937.

Lutra lutra L.

EUROPEAN OTTER

The European otter usually breeds once a year, in winter, in the wild, but young have been born at all seasons. In captivity heat occurs at about 26-day intervals throughout the year. Gestation is 61 to 63 days (1).

1. Cocks, A. H. Proc. Zool. Soc., London, 249–250, 1881.

Martes americana Turton

PINE MARTEN

The pine marten of North America mates in late July and August (1). A single heat period may last 2 weeks (2). At heat the vulva swells and darkens; the swelling is maintained throughout the breeding season and does not regress after an early copulation (3). The litter size is 3 to 5, and the length of gestation, according to some workers, is 220 to 230 days, the

young being born in March and April (4). Others have reported 245 to 265 days (5) so there is apparently considerable variation. The long gestation is caused by delayed implantation of the embryos, and it may be shortened by 3 months if the martens are exposed to increased daily length of light throughout the fall (1).

1. Pearson, O. P., and R. K. Enders. J. Exp. Zool., 95: 21–35, 1944.
2. Cocks, A. H. Proc. Zool. Soc., London, 836–837, 1900.
3. Enders, R. K., and J. B. Leekley. Anat. Rec., 79: 1–5, 1941.
4. Brassard, J. A., and R. Bernard. Canadian Field Nat., 53: 15–21, 1939.
5. Salversen, S. Deutsche Pelztierzucht, 12: 371, 1937.

Martes caurina Merriam

This marten of western North America mates from July 10 to the beginning of September (1) and is monestrous (2). Some mate at 15 months of age, but young are not produced until the female is 3 years old. Copulation is lengthy, lasting 15 to 90 minutes. The litter size varies from 1 to 4, with 2.6 as the mean. In two cases the gestation period was 261 and 276 days (1). Birth occurs from April to June (3).

1. Markley, M. H., and C. F. Bassett. Am. Midland Nat., 28: 604–616, 1942.
2. Grinnell, J., J. S. Dixon, and J. M. Linsdale. Fur Bearing Mammals of California. Berkeley, 1937.
3. Bailey, V. North American Fauna, No. 55, 1936.

Martes foina Erxleben

STONE MARTEN, BEECH MARTEN

In England the stone marten mates in July and August, and the gestation period is 8½ to 9½ months (1). In India mating is said to occur in February, and the gestation period is 9 weeks. The litter size is 4 to 5 (2). If the Indian record is correct, it would suggest that delayed implantation is the rule in the northern part of the range and not in the southern. In view of the fact that increased daylight in the fall shortens the gestation period in *M. americana* this would not be surprising.

1. Fairfoul, D. Brit. Fur Farmer, Jan., 84–85, 1934.
2. Blanford, W. T. The Fauna of British India, Including Ceylon and Burma. Mammalia. London, 1888–91.

Martes martes L.

EUROPEAN PINE MARTEN

The European pine marten is said to be seasonally polyestrous with mating in July. Heat lasts 3 to 4 days and recurs 3 to 4 times at intervals of 3 to 7 days. The duration of pregnancy is 270 to 285 days, and the litter size 1 to 4 (1).

1. Schmidt, F. Zeit. f. Säugetierkunde, 9: 392–403, 1934.

Martes pennanti Erxleben

FISHER

The fisher, a native of North America, reaches puberty in both male and female at 1 year of age, but conception does not occur until it is 2 years old (1). Mating is in April, and gestation lasts 51 weeks. The females mate again a week after whelping. The litter size is 1 to 5, with an average of 3 (2). In 15 cases the range of gestation was 338 to 358 days, with a mean of 352 days (3).

1. Douglas, W. O. Am. Fur Breeder, 16: 18, 20, 1943.
2. James, C. S. Am. Fur Breeder, 13(8): 14–15, 1941.
3. Hall, E. R. Calif. Fish and Game, 28: 143–147, 1942.

Martes zibellina L.

SIBERIAN SABLE

The Siberian sable has a mating season from mid-June to the beginning of August (1). Heat lasts 2 days, and, during the season, it recurs 3 to 4 times

at 9- to 12-day intervals. At the time of heat the vulva reddens. The testes swell enormously during the rutting season. Mating is lengthy, lasting on the average 50 minutes, with a range from 10 to 150 minutes. The duration of pregnancy is 270 to 285 days, and the litter size is 1 to 4 (2). Delayed implantation is the rule, with gestation varying from 249 to 299 days, usually 270 to 275 days (1). Sexual maturity is reached at 2 years (3).

1. Zitkov, B. M. Zool. Ž. (Mosk.), 21: 245–250, 1942.
2. Schmidt, F. Zeit. f. Säugetierkunde, 9: 392–403, 1934.
3. Ponomarev, A. L. Zool. Ž. (Mosk.), 17: 482–504, 1938.

Meles meles L.

EUROPEAN BADGER

The European badger breeds late in July and early in August. Implantation does not occur until January, and in the interval the blastocyst lies free in the uterus. Birth is in March (1,2).

1. Fischer, E. Verh. d. Anat. Ges., Anat. Anz., 71: 22–34, 1931.
2. Fries, S. Zool. Anz., 3: 486–492, 1880.

Mephitis mephitis Schreber

SKUNK

The common skunk of eastern North America mates mostly in the first two weeks of March. The young are born about the second week of May. Proestrum lasts for 4 days, but the vulva is not swollen at this time. Heat also lasts 4 days, and the vulva is swollen. Gestation lasts 62 days from the first mating (1). The number of young is 4 to 7 (2).

1. Wight, H. M. J. Mammalogy, 12: 42–47, 1931.
2. Hamilton, W. J., Jr. The Mammals of Eastern North America. Ithaca, 1943.

Mustela erminea L.

STOAT, ERMINE

The European stoat or ermine comes in heat during the season after its birth, i.e., at 1 year of age. The periods begin in May or June, and ovulation is spontaneous. They continue at intervals of not less than a month, but young stoats do not become pregnant until the following year. Pregnant females are found only in March and April. They come in heat and ovulate but do not become pregnant during lactation. Further ovulations and infertile cycles continue later in the year. At these times 8 to 10 follicles rupture, but the corpora lutea of these infertile cycles are much smaller than are those of pregnancy. The vulva swells during heat, but it does not become as conspicuous as that of the ferret, and the vaginal epithelium cornifies. The average number of embryos is 9, with a range of 6 to 13. The male is sexually mature at 1 year. There is a rapid enlargement of the testes to 13 times their former weight from February to March, but retrogression sets in from July onward, and no spermatozoa can be found by October (1).

Birth is in April and an observed pregnancy lasted 10 months, consequently delayed implantation is probable (2).

The American subspecies, *M. e. cicognanii* Bonaparte, comes in heat in the early summer (3) and the young are born between mid-April and early May. The testes begin their growth in February or March (4).

1. Deansley, R. Trans. Roy. Soc., London, 225B: 459–492, 1935.
2. Grigorjev, N. D. Zool. Ž. (Mosk.), 17: 811–814, 1938.
3. Hamilton, W. J., Jr. The Mammals of Eastern United States. Ithaca, 1943.
4. Wright, P. L. J. Exp. Zool., 91: 103–110, 1942.

Mustela furo L.

FERRET

The ferret has a limited breeding season, from March or April until August, and can have 2 or 3 litters during the year (1). Ferrets transported

from England to the Southern Hemisphere bred in October, immediately upon their arrival in Pretoria. In Kenya, almost on the Equator, they experienced heat at the normal time for Great Britain. Afterwards some came in heat twice in the year, others at any time (2). Much work has been done upon the effects of varying the length and intensity of light in this species, and it is summarized later in the section on physiology. In the absence of the male the female may remain in heat for a long time, e.g., from April to August.

Ovulation is induced by coitus, and it occurs about 30 hours afterwards (3). Pseudopregnancy lasts for 5½ to 6 weeks. It is followed by a new heat if it terminates early enough in the season. There is no heat during lactation, but, if the young are removed, heat ensues 7 to 10 days later (4,5). Proestrum is somewhat slow in developing at the beginning of the season. It is characterized by a marked swelling of the vulva, which takes about 2 to 3 weeks to reach its full development. This development is maintained throughout heat, and the vulva at this time is about 50 times the anestrous size. It declines gradually after coitus (4).

The average duration of coitus is about 2 hours (range ¼ to 3 hours). For 36 hours afterwards the vulva remains turgid but it becomes flaccid by about 60 hours. The ovum remains capable of fertilization for not more than 30 hours; from 18 to 30 hours after ovulation only a small proportion are capable of being fertilized, and small litters are produced from matings made at this time (3).

The mean litter size is $8.5 \pm .3$, with a range from 5 to 13, and the duration of gestation is 42 days from mating with practically no variation (4).

HISTOLOGY OF THE FEMALE TRACT

OVARY. During anestrum the ovary contains only small follicles, but during proestrum these grow at a rate corresponding to that of the vulva. The maximum size of the ripe follicle is about 1.4 mm. The fully formed corpus luteum measures about 2 mm., and during pregnancy or pseudopregnancy the ovaries consist almost entirely of luteal tissue. The corpora lutea persist throughout pregnancy and degenerate rapidly at its end. There is no corpus luteum of lactation. The ovary contains much interstitial tissue, but it is not so abundant as it is in the rabbit (4).

VAGINA. The vaginal epithelium just after the end of the breeding sea-

son consists of 2 to 3 layers of low columnar epithelial cells. Just before the beginning of the season the epithelium grows and cornifies to some extent, while the connective tissue is compact. In proestrum several squamous layers of epithelium develop with some cornification. This is at the time that the vulval swelling begins. In heat the epithelium is thicker, and there is much cornification. The connective tissue is very spongy, and it has many elastic fibers embedded in it. In pseudopregnancy the epithelium is stratified high columnar. Few cornified cells remain, and the surface is rough. The connective tissue remains spongy. At the end of pseudopregnancy the appearance is similar except that many lymphocytes are present (6). When cornification sets in, it begins in the upper part of the vagina and progresses toward the vulva. Growth is most active during early heat, and there is no sudden appearance of leucocytes at its end (7). There is no true cornified stage in the vaginal smear (5).

UTERUS. In anestrum the endometrium is thin, with compact, undeveloped glands, while the epithelium is low cubical. In proestrum cell divisions are abundant. Congestion is marked, and there may be some extravasation of blood, which passes through lacunae in the epithelial layer into the lumen. There is some suggestion, however, that this occurs only in the heat period soon after parturition. During heat the glands have large lumens and are secreting. The glandular cells are large, and those of the epithelium are tall columnar. The mucosal layer is somewhat folded. In pseudopregnancy there is a great development of the glands with the result that the endometrium becomes lacelike, resembling the condition in the rabbit. At the height of this condition giant cells tend to form in the crypts of the glands. Degeneration, indicated by the sloughing off of cells and accumulation of debris, begins at about 5½ weeks of pseudopregnancy (1,4).

PHYSIOLOGY OF THE FEMALE TRACT

If ferrets receive illumination during the evenings beginning October 12, most females come in heat in December, 3 months earlier than usual, and they may become pregnant (8). This response is limited to a band in the spectrum extending from red λ 6,500 to λ 3,650 in the near ultraviolet. Within this range intensity is more important than the wave length. Females subjected to incomplete darkness did not come in heat at the proper time unless

proestrum had already begun, in which case the usual changes followed (9). The degree of acceleration is related to the intensity of light (10), and it is not produced if the optic nerves are cut (11). However, intensity or duration of light is not wholly the explanation of emergence from anestrum, since females kept in darkness for 23½ hours each day from the end of January mostly underwent the usual vulval development but took longer than usual (12).

Ovulation may be induced in the unmated estrous ferret by the injection of a gonadotrophic preparation. The dose needed is about the same as that required to induce ovulation in the rabbit; hence, weight for weight, the ferret requires more than the rabbit (13). The considerable length of copulation in the normal course of events raises the question how soon sufficient stimulus has been given to cause the release of an adequate quantity of gonadotrophe from the pituitary. If coitus is interrupted after 15 to 20 minutes ovulation follows in 90 per cent of cases, and it has been found that sexual excitement, i.e., the presence of the male with the female in heat, without coitus, occasionally produces ovulation. If hypophysectomy is performed 1¾ hours after the start of coitus, which lasted 1¼ hours in these cases, ovulation is not usually interrupted, but if it is done within an hour of the start, following an interrupted coitus, ovulation does not occur. Sufficient gonadotrophe has not been released, therefore, within an hour of the beginning of copulation (14,15). Hypophysectomy during anestrum causes but little further atrophy of the genitalia. The onset of new heat periods at the usual time is prevented by the operation, and increased light is without effect. Estrogens produce the usual effects upon the uterus and the vulva. The latter requires more than the uterus, which is also the case in normal anestrous ferrets (16,17).

The injection of P.M.S. during anestrum causes the rapid development of quiescent follicles. With moderate doses the response is almost purely follicle-stimulating without ovulation or corpus luteum development. With larger amounts thecal luteinization follows the injections (18).

Hysterectomy does not cause prolongation of the life of the corpora lutea, and it has no effect upon other reproductive phenomena (19).

The injection of estrogens causes the pubic symphysis to open (20).

If females become pregnant or pseudopregnant at the end of the usual breeding season, these conditions are maintained and last the normal length of time, despite the fact that normally the female would be in anestrum (21).

THE MALE

In October the testis and epididymis are at their lowest level. In November and December their weights begin to rise to a peak, which is reached early in March. Their weights fall again rapidly in August. The weight of the penis follows a similar curve, but the individual variability is greater. There is no spermatogenesis in October, when the tubules are small, and only Sertoli cells and spermatogonia are present. Renewed activity begins in November; spermatocytes are found in December, spermatids in January, and spermatozoa at the beginning of February. Interstitial cells are largest in February and smallest in November (22). After hypophysectomy the testes retrogress to the anestrous level within about a month (23).

Immature ferrets kept on a "short day" light regime reach puberty later than usual; a "long day" accelerates its onset, but this is followed by an early regression (24), even though the increased amount of light be continued. The interstitial tissue of the testis is more sensitive than the spermatogenic; it is earlier to respond and later to regress (25).

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Mustela nivalis L.

EUROPEAN WEASEL

In the male weasel there are no vesiculae seminales and no obvious prostate. The testes descend to the scrotum at an early age and remain there throughout life. The male is sexually mature when 4 months old, i.e., in August, as birth is in April. By December the testes are quiescent in young weasels, but adults have no spermatozoa by the end of October, though spermatocytes are present at all times. The interstitial cells increase to twice their former diameter during the breeding season, and the accessory organs change in harmony with them (1). Since the reported periods of gestation are most variable, delayed implantation may be suspected.

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Mustela putorius L.

STOAT

The common European stoat has one litter a year, in March or April, followed by mating and ovulation. Implantation is delayed, and pregnancy lasts 9 to 10 months (1).

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PLATE IX. Ovarian changes, *Microtus pennsylvanicus*. *Top:* Proestrum, large follicle with ovum. H and E. x100. *Center:* Diestrum, ovary nearly filled with corpora lutea. H and E. x10. *Bottom:* Diestrum, lutein cells. H and E. x100.

PLATE X. Copulation plug, chinchilla. Note lining of cornified vaginal cells. H and E. x10.

Mustela vison Schreber

MINK

The North American mink is apparently polyestrous in the sense that several waves of follicles ripen in the absence of ovulation. The breeding season begins in March and 3 heat periods of about 2 days each occur at intervals of 8 to 9 days (1). Heat is said to be 10 days earlier in the season in the eastern than it is in the Yukon strain (2). Ovulation is induced by coitus, and it occurs 42 to 50 hours afterwards. If no ova are ripe at this time, later ovulations are inhibited (3). The duration of coitus is 30 to 40 minutes. If pregnancy does not result, the female become pseudopregnant (2). The diameter of the ovum is 107 μ (4). The length of gestation is from 39 to 76 days, with a mean of 50.95. The later in March the mating is made, the shorter is the pregnancy (5); this suggests a slight delay in implantation following earlier matings. Another average was 53 days (1), and a range of 45 to 60 days had been reported (2). Embryonic attachment is said to last less than 31 days, and the variability of the length of gestation, together with the fact that it is shortened by 3 days if the mink are exposed to longer hours of light, strongly suggests delayed implantation (6). The litter size ranges from 4 to 10 (2).

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Taxidea taxus Schreber

AMERICAN BADGER

The American badger mates late in summer, from August to September; implantation does not occur until about February 15, and the young are

born about April 1 (1). In the west birth usually occurs in February at sea level, but not until April or May in the mountains. The litter size is 1 to 4 or 5 (2).

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Other MUSTELIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Aonyx capensis Schinz Cape Clawless Otter			2–5, usually 2–3	About 63 days	Africa
Conepatus mapurito Gmelin Chilean Skunk				42 days	
Eira barbara L.			3–4		S. America
Enhydra lutris L. Sea Otter	No fixed season, but most frequently late spring (Barabash-Nikifarov)		1	240–270 days	N. Pacific. Mates in water
Gulo luscus L. Wolverine	March–Apr. (Wallace)	April–June	1–5, usually 2–3	60 days	Canada
Ictonyx striatus Perry Striped Polecat		Jan.–March in Giza Zoo (Flower)	2–3		Africa
Mellivora capensis Schreber Honey Badger, Ratel			2	About 6 months	Africa
Mephitis hudsonica Richardson Northern Plains Skunk	Early March (Seton)	End April to early May	4–7		Western N. America
M. macroura Lichtenstein			5		Southwestern N. America

Other MUSTELIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
M. mesomelas Lichtenstein	Apr.–May (Cuyler). One litter a year (N.A.F. 55)		4–5		Central and southern N. America
M. occidentalis Baird Western Skunk		May–June (N.A.F. 55)	6–12		Western N. America
Mustela alpinus Gebler Pale Weasel	Feb. (Blanford)	May	1–5		Asia
M. eversmanni Lesson Steppe Polecat				36–37 days	Europe
M. frenata Lichtenstein Large Brown Weasel	July (Hamilton). Testes enlarge Feb.–Mar. (Wright)	Mid-April	4–8		Southwestern N. America. Delayed implantation 21–28 days before birth (Wright)
M. larvatus Hodgson Tibetan Polecat		April (Blanford)	5–7	9 weeks	Himalayas
M. noveboracensis Emmons New York Weasel	Testes enlarge late March–Apr. (Hamilton)			About 70 days	Eastern U.S.
M. rixosa Bangs Least Weasel		Oct., Jan., Feb. (Hamilton)	3–6		Northern N. America
M. sarmaticus Pallas Mottled Polecat		March–April (Blanford)	3–4		Eastern Europe, western Asia
Poecilogale albinucha Gray African Striped Weasel			2		Cent. and S. Africa

Other MUSTELIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Spilogale gracilis Merriam Spotted Skunk			4–5		Western and southwestern N. America
S. indianola Merriam Gulf Spotted Skunk	Late winter (Hamilton)	Early spring	4–5		Gulf of Mexico

CANIDAE

Canis familiaris L.

DOG

The domestic dog is monestrous and usually has two heat periods in a year, in late winter or early spring and in the fall. Proestrum lasts for about 7 to 9 days and is characterized by a swelling of the vulva and a discharge of blood derived from the uterus. Estrus lasts about the same time, and about 1 day after its commencement the ova are shed. These are almost unique in that the first polar body is not shed, and fertilization is apparently not possible, until some time after they have left the graafian follicles. If the bitch does not become pregnant, the corpora usually persist for about 2 months, during which time a condition of pseudopregnancy exists. This period is followed by anestrum lasting about 2 months.

THE ESTROUS CYCLE

The bitch is usually said to have two heat periods a year, one in the early spring and one in the fall. Curves of births according to seasons made from data in kennel club records do not show this fact. The curves are almost unimodal, with peaks denoting conception very early in the spring. The

true nature of the breeding season is obscured in these records by the breeders' habit of mating their dogs usually in spring and by the method of estimating dogs' ages, which makes it advantageous for show and racing purposes to have them born early in the year. However, a series of American records for several breeds shows a slight bimodality, with most conceptions in February and April (1), and similar records for greyhounds in England have similar peaks in January and March (2). It is not clear whether these are natural phenomena or the result of breeding customs. Puberty is reached at 6 to 8 months (3).

The onset of heat in the dog is gradual and is preceded by a long proestrum, which is marked by considerable swelling of the vulva and bleeding from the uterus. The length of proestrum varies somewhat widely. One series gives for greyhounds 7 to 22 days, as judged by erythrocytes in the vaginal smear (4); another, from the first appearance of a sanguineous discharge to first acceptance, gave 4 to 13 days with a mean of $9 \pm .5$ days (5). Heat in the greyhound lasts 7 to 9 days (4), and for a limited series of dogs of various breeds 4 to 13 days; mean, $9 \pm .5$ days (5). There is often an overlapping of the external signs of the two periods. During the proestrum the male and female are interested in each other, but coitus is not usually allowed until the last day or two of bleeding. Ovulation is usually 1 to 3 days after first acceptance by the male (4,5). The dog and fox differ from other mammals so far investigated in that the first polar body is not extruded from the ovum for some days after it has been shed. Accordingly the ova are apparently not ready for fertilization for some days after ovulation (6), which is spontaneous (7).

There is some uncertainty concerning the length of time during which the eggs may be fertilized after they have been shed. It is certain that they may survive for 4 days, and probably for twice this time. They travel quickly to the middle of the oviduct, taking a day or less, then they remain in this part, or in the portion nearest the uterus, for several days (5).

After ovulation corpora lutea are formed, which persist, in the absence of pregnancy, in a functional condition for at least 30 days. Then they gradually degenerate, but they may be detected in the ovaries at the time of the next heat. This persistence is accompanied by proliferative changes in the uterus and mammary glands, and the decline is marked, in many cases, by lactation and the formation of a nest, a usual reaction at the end of a true pregnancy (5,8). The duration of this pseudopregnancy is somewhat variable

and is usually given as about 2 months. Probably it is too gradual to set any definite limit.

There appears to be practically no precise information on the litter size of the dog and of its variation with the breed. For the German sheep dog the mean litter size is $7.15 \pm .02$, with a range from 1 to 17. The sex ratio in this series, which is drawn from stud books, was $52.75 \pm .12$ per cent males. It tends to decrease with litter size. The material is peculiar in that there are too many combinations, exclusively or predominantly, of one sex (9). This may indicate that uniovular twins are frequent. In another study of the German sheep dog, in which the mean litter size and its range were the same as in the work just quoted, 83 per cent of the litters were between 4 and 10. Stillbirths were 2.29 per cent of the total, and their sex ratio was 62.25 per cent (10), which suggests that the sex ratio may be higher early in gestation than at birth, a condition which holds also in man and the pig. In the same paper the sex ratio for the schnauzer is given as 50.5 per cent, and for the French bull, 50.4 per cent, but for bull terriers the ratio has been recorded as 55.9 per cent (11).

The gestation period is usually given as between 58 and 63 days (7,3).

HISTOLOGY OF THE FEMALE TRACT

OVARY. At the beginning of the proestrum large numbers of small- and medium-sized graafian follicles can be found in the cortical zone of the ovary, but most of these already show degenerative changes, and very few are destined to rupture. Those follicles which continue to grow have folds of granulosa cells with vascularized cores of theca interna, which are more complex than those found in any other mammal that has been investigated. As the bitch enters heat, these folds become more complex, but the theca interna cells show less than the usual amount of hypertrophy. Ovulation usually occurs on the first day of heat or acceptance, when the follicles are about 6 mm. in diameter, and there is little growth during proestrum. All rupture within a short time. At first the granulosa lutein cells are arranged in irregular columns resembling an open lacework. By the eighth day the appearance is more compact, although large cavities are still present, and the corpora lutea do not become completely solid until they are about 18 days old. The condition of the uterus indicates that they remain functional for 30 days after heat has ended, but histologically the cells remain in good condition for some time longer. When the decline

sets in, it is so gradual a process that one cannot give a time for their effective life on histological grounds alone (5,12).

The average size of the ova after they have been shed is $77 \times 90\ \mu$ excluding, and $95 \times 110\ \mu$ including, the zona pellucida.

VAGINA. One feature of proestrum is the marked edematous swelling of the vulva, which increases throughout this period and remains during heat, after which the decline is somewhat gradual. The vestibule is coated with low stratified epithelium, which increases a little in height during proestrum, but never to any great extent. The vagina proper exhibits well-marked changes during the cycle. During anestrum the epithelium is columnar in type, 2 to 3 layers thick. By the beginning of proestrum it has become flat stratified, 6 to 8 layers thick. It continues to grow, so that by first acceptance it is 12 to 20 cells thick, and the superficial layers have become cornified. Cells are being lost from the superficial layer throughout, but marked desquamation does not set in until the third or fourth day of heat, when reduction is rapid. At this time there is also some infiltration of leucocytes. Repair sets in soon after heat is over, and by the tenth day postestrum the epithelium is of the anestrous high columnar type.

The vaginal smears are clear-cut, with red blood cells and epithelial cells in early proestrum. The latter type gives way entirely to large cornified cells and, after bleeding ceases, these are the only cells present. Toward the end of heat a few leucocytes are found, but they do not become abundant until 2 to 3 days after heat has ceased. The anestrous smear consists of epithelial cells with a few leucocytes (5).

UTERUS. During anestrum the endometrium is low and compact, but the glands are poorly developed. The lumen of the uterus is H-shaped in cross section. In proestrum the endometrium becomes very edematous, the lumen flattens out, and hyperemia is very apparent. Focal bleeding occurs, but, as the epithelium does not rupture, the erythrocytes escape into the lumen by diapedesis. Mitoses are abundant throughout, but the glands remain simple. During heat the edema persists, but bleeding ceases and hyperemia is not so apparent. The glands are increasing in complexity and show some secretory activity. Leucocytes are abundant at this time. During pseudopregnancy the endometrium is in two well-defined zones, a superficial "compacta" and a deep "spongiosa" with numerous branched glands. The zona compacta develops villous processes which obstruct the uterine cavity. Retrogressive changes set in at the twentieth day after heat has ceased, and they become marked by the thirtieth day; but the process of involution

is gradual, and the anestrous condition is not reached until 85 days (3,5,8,12). It is said that the end of pseudopregnancy is marked by a further extravasation of blood (8), but this has not always been found (5).

Much dark pigment is present in the superficial layers of the uterus in anestrum and proestrum (7), and during the latter period many pigment-laden macrophages are found (12).

During proestrum the epithelium of the oviduct is tall columnar and it is secreting. There are variable numbers of cilia. During heat the picture is the same. After heat is over, secretion ceases; the cells are not granulated but are vacuolar. Cilia are much less apparent. In anestrum the cells are low, nonciliated, and they contain some granules (3,13).

True basophil cells are not present in the anterior pituitary, but two types that seem to be essentially basophilic have been described. A large granulated type increases during proestrum, and these cells become heavily granulated. They degranulate before ovulation and are present in small numbers during the lutein phase of the cycle. Eosinophils are also degranulated during this phase. All granular types increase gradually during anestrum. There are no specialized pregnancy cells (14).

PHYSIOLOGY OF THE FEMALE TRACT

The pH of the fluids secreted into a closed uterine segment of a bitch brought into heat with stilbestrol was 6.09 with a range from 5.19 to 6.26 (15).

The uterine muscle responds to epinephrin by contraction if the bitch is pregnant, i.e., if a corpus luteum is present, and by relaxation at other times (16). This is a peculiarity shared by the cat and the cow.

Estrogens can be detected in the urine during pregnancy after 15 to 18 days, but the level is not high at any time (17). Twenty I.U. daily of estrogen is without effect in the immature bitch, but 200 I.U. produces cornification in the vagina. The same daily dose in the mature spayed female produces the usual changes of heat and of proestrum (18). Brief microscopical bleeding follows ovariectomy in metestrum, after an interval of 7 to 16 days, and the injection of 1,100 R.U. or more of estrogens into spayed females produces macroscopic bleeding from an endometrium resembling that of proestrum (19). This reaction occurs in the absence of the pituitary and is therefore probably a direct one upon the uterus (20).

Since cornification of the vagina has been produced by the injection of

estrogens during anestrum without vulval swelling or proestrous bleeding, it probably has a much lower threshold dose than these other changes (21).

Glandular growth in the uterus may be induced by the injection of 3 to 5 Rab.U. daily of progesterone for 5 to 6 days (18). Ovariectomy during pregnancy is followed by reabsorption of the embryos or by abortion. However, none of the operations were performed during the second half of the period (7). Hypophysectomy at 5 to 7 weeks produces the same effect (22).

The injection of 100 M.U. of gonadotrophic hormone during anestrum produces heat and ovulation (23).

THE MALE

The amount of semen ejaculated is said to be about 20 cc. (1), which, inasmuch as the dog has no vesiculae seminales, is a considerable amount. Doubtless there are large breed differences. The urethral glands produce less than 2 per cent of the amount yielded by the prostate. After castration secretion by the prostate ceases in 7 to 23 days (24). The pH of the semen varies from 6.7 to 7.1 (25). By the uterine fistula method it has been found that spermatozoa are at the uterine entrance to the oviducts 25 seconds after ejaculation (26). Copulation is a somewhat prolonged process and spermatozoa have been found throughout the oviduct 20 minutes after it began (1). They are able to live in the female tract for 48 ± 12 hours (4).

The injection of 50 I.U. of androgen daily in 1-month-old puppies caused growth in the accessory organs, mostly in the prostate and vas deferens (27).

The ejaculate of the dog does not coagulate, and it has been found to contain a fibrinogenase which destroys the clotting power of blood plasma (28).

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Canis latrans Say

NORTHERN COYOTE

The common coyote of North America experiences one breeding season a year (1), and the age of puberty is usually 2 years. In one case bleeding from the vagina was first noted December 11; it became more rapid and brighter on January 19, but attempts by the male to mount were rejected. On February 6 the vulva began to swell; it reached its maximum development by the eighth. The female allowed coitus for the first time on February 24, and on February 27. This suggests a long proestrum and a heat period lasting about 4 days (2). Normally the female sexual season begins in February and ends in April. The testes begin to show activity in November. In January spermatozoa are present and the epididymis is enlarging. The testes gradually recede from March onward, and by the end of May there are no spermatozoa. The time of minimal activity is reached in November (1).

The average number of embryos is 6.23 (1,330 cases), and the average num-

ber of den young is 5.70 (1,582 cases) (1). The period of gestation is 60 to 65 days (1,2). Another series of embryo counts gave a mean of 6.66 ± .11 (3).

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Nyctereutes procyonides Gray

DOG RACCOON

The mating season of the Asiatic dog raccoon begins in February (1), and the duration of heat is 6 to 8 days. It is shown externally by swelling of the vulva and of the nipples (2). The gestation period is 61 to 63 days, and the litter size varies from 5 to 12, with 7 to 8 as the modal number (1).

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Vulpes fulva Desmarest

RED FOX, SILVER FOX

The specific name, *Vulpes fulva,* is taken to include most domesticated foxes, and it probably should include several wild varieties, such as *V. regalis* Merriam and *V. macroura* Baird, which have sometimes been described as subspecies.

The fox is monestrous, with one season a year, from December to March with most matings in late January and February, though the blue fox is said to be somewhat later than the silver fox, i.e., from February to March (1). Foxes breed in the first year following their birth (2). Proestrum and estrus lasts 12 to 14 days, and during this time there is some swelling and whiteness of the vulva. Sexual receptivity lasts for 2 to 4 days (3). Fifty-three per cent of matings occur between 5 A.M. and 10 A.M., and 20 per cent from 10 A.M. to 1 P.M. (4). Ovulation is spontaneous, and it occurs most frequently on

day 1 or early on day 2 of sexual receptivity. The effects of mating on specific days upon the chance of pregnancy and upon litter size are given (5):

	Percentage of pregnancies	Average litter size
Mating on day 1	54	1.77
Mating on day 2	96	3.98
Mating on day 3	86	3.79

It has also been stated that mating on the first day of vaginal cornification produces significantly larger litters than matings either before or after this day (6).

There is no bleeding during proestrum, which is, therefore, not well defined. If pregnancy does not result from mating, or if the female is not mated, she becomes pseudopregnant, denoting a fairly long life for the corpus luteum (2,7).

The mean litter size is $4.52 \pm .03$, with a distribution of 1 to 8, mode 4 to 5, and standard deviation, 1.35 (2). On German fox farms the average was $3.94 \pm .03$ (8). The litter size rises steadily to 5 to 7 years of age, from an initial level of 4.34 to 4.84, and litters born early in the season tend to be larger than those born later (2). The sex ratio taken during the first week or so after birth was 52.93 ± 1.00 per cent males (2). The length of gestation is from 49 to 55 days, with a pronounced mode at 52 days in all the data. Means are 51.99 ± 0.036 (2), 52.74 (6), 52.07 (9), and $52.12 \pm .006$ (4). There is a slight tendency for small litters to have a longer gestation (2).

HISTOLOGY AND PHYSIOLOGY OF THE FEMALE TRACT

The fox resembles the dog in that the first polar body is not extruded from the egg until after ovulation. Accordingly, fertilization does not occur until at least one day after ovulation (10). At 2 to 3 days before acceptance of the male the largest follicles are 4 mm. in diameter. The granulosa is thin and is folded in the manner found in the ripe follicle of the dog. At first acceptance the follicle measures 7 mm. in diameter. The ovum measures $104 \times 76\ \mu$. Fertilization takes place in the middle section of the oviduct (11).

The vaginal smear always contains some epithelial cells, and there is a gradual increase in cornified cells during proestrum, with a maximum at day 1 of heat. On that day leucocytes are absent; then they appear and gradually increase in numbers (12).

The pH of the vaginal secretions in early proestrum is 6.3, and during heat it is 7.9 (3), an unusual reversal.

Vixens may be brought in heat in September and October by the injection of 250 to 340 M.U. of prolan (pregnancy urine extract), judging by the vulval swelling and vaginal smears (13). However, heat is only induced by this means late in anestrum when the follicles are in the antrum stage. Ovulation is rarely induced (14). Other results have not been promising as it is said that single doses of gonadotrophe will not induce heat and that repeated doses are harmful to the ovaries (15).

THE MALE

The testes retrogress and spermatogenesis ceases during the anestrous period. Spermatogenesis begins in November, and the male is fertile 8 to 10 weeks before the breeding season begins. In their first season, in England, spermatogenesis in young foxes is complete by the end of November (16,17). The left testis is the longer and heavier, and the right is broader and thicker. The sperm head measures $8 \times 5\ \mu$, and the entire length is $60\ \mu$ (17). According to one report, in the United States spermatozoa can be found at all seasons, but outside the breeding season most tubules are inactive (18). During January there is a marked development of the prostate gland, which increases from 0.5 cc. to 5 to 6 cc. in volume. In young males the development of the testes and accessories lags 2 weeks behind that in mature males.

In mature males the average ejaculation is 6 cc., with a range from 0.1 to 33 cc. The concentration of spermatozoa is 55×10^6 per cc. (3), and the pH of the semen is 6.2 to 6.4 (19).

Mating usually lasts 15 to 25 minutes, and spermatozoa may be found in the oviduct within 8 minutes after unlocking. Artificial insemination into the vagina is unsuccessful, and it is impossible to deposit semen in the cervix because of the minute curved passage in the spongy papilla (6).

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Vulpes vulpes L.

ENGLISH RED FOX

The English red fox, like *Vulpes fulva,* is monestrous, with the mating season at the end of January. It breeds first at about 10 months of age. Ovulation is spontaneous. There are few or no vulval signs of approaching heat, and no premature follicular growth during anestrum. The ovum measures $110 \times 125\ \mu$. The unmated vixen passes into pseudopregnancy after she has been in heat. The litter size varies from 3 to 7, and corpus luteum counts in 6 vixens averaged 5.7 (1). In proestrum the vaginal epithelium is many-layered, and the stroma of the uterus is dense and vascular. In pseudopregnancy the uterine stroma is not so dense; the glands are coiled, mainly at their bases, and their lumens are practically obliterated, as is also the uterine lumen. At the end of this period the surface epithelium of the uterus breaks down (1).

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Other CANIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Alopex berengarius Merriam Arctic Fox	Feb.	May–June	4–8, usually 6–7; mean 6.2 ± .2	52 days	

Other CANIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
A. lagopus True Arctic Fox				60 days	Northern N. America
A. pribilofensis Merriam Pribilof Arctic Fox	March–April (N.A.F. 46)	May 17–June 6	5–11		
Canis azarae Wied Azara's dog	Winter (Rengger)				Paraguay
C. dingo Blumenbach Dingo			3–5, usually 3	63 days	Australia
C. indicus Hodgson Jackal			4	63 days	India
C. lupus L. European Wolf	Dec.–Apr. (Blanford)		4–9	63	Europe and Asia. Puberty, 2 yrs.
C. lycaon Schreber Timber Wolf		March–Apr. (N.A.F. 55)	1–12, av. 6	9 weeks	Eastern N. America
C. mexicanus L. Gray Wolf		March (N.A.F. 49)	6–10		S. Mexico. Puberty, 2 yrs.
C. occidentalis Richardson Gray Wolf	End Jan. to 1st March; later if colder (Seton)		3–13, usually 6–7	63 days	
C. ochropus Eschscholtz				65 days	California
C. pallipes Sykes Indian Wolf		Oct.–Dec., chiefly Dec. (Blanford)	3–8	63 days	India

Other CANIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Chrysocyon brachyurus Illiger Maned Wolf			2		S. America
Cuon dukhunensis Sykes Indian Wild Dog	Winter (Blanford)	All seasons, mostly Jan.–Feb. (Brander)	2–4	63 days	India
Lycaon pictus Temminck Cape Hunting Dog	No regular season, but may be spring and fall in temperate climates (Shortridge)		2–6	63? 80? days	Africa
Otocyon megalotis Desmarest Big-eared Fox		Dec.–Apr. (Wilhelm)	3–5	60–70 days	Africa
Thos adustus Sundervall Side-striped Jackal		Winter in Transvaal (S. Hamilton)	3–7	57–60 days	Africa
T. mesomelas Schreber Black-backed Jackal		Nov.–Dec. (Wilhelm)	2–6		Africa
Urocyon cinereo-argenteus Schreber Gray Fox	Feb., monestrous (Grinnell)	March–May	2–7, av. 4	About 63 days	N. America
Vulpes alopex L. Common Fox	End of winter (Blanford)	End March, April	5–7	9 weeks	
V. bengalensis Shaw Indian Fox	Nov.–Jan. (Blanford)	Feb.–Apr.	4		Europe and Asia

Other CANIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
V. chama A. Smith Chama Fox		Aug.–Sept. (Shortridge)			S. Africa
V. velox Say Kit Fox			4–5		N. America
Fennecus zerda Zimmermann Fennec				51 days	N. Africa

VIVERRIDAE

Civettictis civetta Schreber

AFRICAN CIVET

This civet of tropical Central Africa has two breeding seasons a year in Tanganyika, in March and October. The litter size is 2 to 5. More secretion can be obtained from the scent glands of the male at the time of rut than at other times (1).

1. Vandenput, R. Bul. Agric. Congo Belge, 28: 135–146, 1937.

Other VIVERRIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Atilax paludinosus Cuvier Water Mongoose		Aug.	2		Africa

Other VIVERRIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Cynictis penicillata Cuvier Bushy-tailed Mierkat			2–4		S. Africa
Genetta genetta L. Small Spotted Genet		Sept.–Oct. and March–May, in S. Africa (Shortridge)	2–4, usually 2–3		Africa
G. tigrina Schreber Rusty-spotted Genet		May and Oct., in S. Africa (Shortridge)	2–3		Africa
Helogale parvula Sundervall Dwarf Mongoose		March (Shortridge)	2–4		S. Africa
Herpestes edwardsi Desmarest Common Mongoose	Probably all year (Frere)		2	About 60 days	India
Mungos mungo Gmelin Banded Mongoose		Spring (Blanford). Pregnant Nov., Dec. in S.W. Africa (Shortridge)	3–6		Africa and India
Myonax cauui A. Smith Slender Mongoose			2–3		Cent. and S. Africa
M. sanguineus Rüppel Little Mongoose			2		Cent. Africa
Paracynictis selousi De Winton Mierkat			2		Northern S. Africa
Paradoxurus grayi Bennett Himalayan Palm Civet			4		Northern India

Other VIVERRIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
P. niger Desmarest Palm Civet			4–6		India
Prionodon pardicolor Hodgson Spotted Tiger Civet	Feb., Aug. (Blanford)		2		Eastern Himalayas into China
Suricata suricatta Erxleben Slender-tailed Mierkat		Pregnant Nov., Feb. (Shortridge)	2–4		S. Africa
Viverra megaspila Blyth Burmese Civet			1–3		
V. zibetha L. Large Indian Civet	May–June (Blanford)		3–4		S. and S.E. Asia
Viverricula malaccensis Gmelin Small Indian Civet			4–5		S. and S.E. Asia

PROTELIDAE

Proteles cristatus Sparrman

AARD WOLF

The African aard wolf bears its young in the southern part of its range during the months of November and December. The litter size is usually 2 to 4, but as many as 6 may be born at one time (1).

1. Shortridge, G. C. The Mammals of South West Africa. London, 1934.

HYAENIDAE

Crocuta crocuta Erxleben

SPOTTED HYENA

The hyena of Africa is polyestrous all the year, with a cycle of about 14 days. There is no seasonal sexual activity in the male. The female reaches puberty at a later age than the male. She has a peniform clitoris, scrotal pouches, and perineal and anal glands, resembling those of the male. The resemblance is so great that the ancients regarded the hyena as hermaphroditic. The corpus luteum is functional throughout pregnancy and persists during lactation. The number of young is 1, rarely 2, but a larger number of eggs are shed, apparently from only one ovary. The duration of pregnancy is 110 days (1). In South Africa the young are said to be born in winter (2).

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Other HYAENIDAE

SPECIES	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Hyaena brunnea Thunberg Brown Hyena	2–4	3 months	S. Africa. Testes external
H. hyaena L. Striped Hyena	3–4		N. Africa and Asia

FELIDAE

Felis catus L.

DOMESTIC CAT

The domestic cat reaches puberty at about 15 months of age. She is, in a sense, seasonally polyestrous, since in the absence of the male several heat

periods are experienced, in spring and in early fall. Ovulation is induced by coitus and rarely occurs in its absence. Sterile copulation produces a condition of pseudopregnancy which lasts for 36 days. The modal litter size is 4, and the period of gestation is about 63 days from coitus.

THE ESTROUS CYCLE

In northern Europe heat periods are experienced twice a year, in spring and early fall (1), but in Algiers the seasons are from December 15 to the end of January, and from July 15 to the end of August. Some females, however, may be found in heat at any time from January to July (2). In the northern United States anestrum lasts from September to January (3). Heat, in the presence of the male, lasts about 4 days, with the time of greatest acceptance on the third day. In the absence of the male it lasts 9 to 10 days (4), or more (1), and it recurs 15 days to 3 weeks later (4). Ovulation is induced by coitus, and in 100 cases without coitus it did not occur (4). It follows coitus after 24 to 30 hours (5), 27 hours (4), or 40 to 54 hours (1). Sterile copulation is followed by pseudopregnancy, which lasts for 36 days, but the corpus luteum regresses from 28 days onward (1). Another report gives about 30 days as the usual duration, but it may last 44 days (3).

The ovum takes 95 to 103 hours from the time of shedding to pass through the oviduct into the uterus. The number of eggs shed is 4.12, with a mode at 4 to 5 (4), and the mean litter size is 3.88. The latter is correlated with the weight of the mother (6). The duration of gestation is 63 days from coitus (4), or 65 days in highly bred cats with little exercise and less in those which are free to roam (7).

HISTOLOGY OF THE FEMALE TRACT

OVARY. During the period between coitus and ovulation there are no obvious changes in the graafian follicle in the first six hours; then the cumulus oöphoron enlarges because of intercellular accumulation of secretion. Later, the whole granulosa layer shares in this enlargement and loosening. The secretion of this secondary liquor folliculi ceases by 24 hours, and then the granulosa cells begin to appear active; they lose their pycnotic appearance and become vesicular. The first spindle in the ovum is formed at 18 hours, and the polar body is extruded at 22½ hours (5). At ovulation there is no hemorrhage or leucocytic invasion into the cavity, but the walls are deeply folded. The theca cells form the interstitial tissue of the corpus luteum;

mitoses are numerous in these cells by 18 hours after ovulation, but few can be found after 7 days. The lutein cells are formed exclusively from the granulosa layers. The maximum size of the corpus luteum is reached at 10 to 16 days after coitus. During pregnancy gradual regression sets in after 20 days (8). This is said to occur after 28 days in the corpus luteum of pseudo-pregnancy. Follicles which do not rupture retrogress by thecal atresia (1), and the interstitial tissue of the ovary originates in the thecal cells (9). There is no evidence for neogenesis of ova during adult life, of for linking the degree of atresia to events in the estrous cycle (10).

VAGINA. The anestrous vaginal epithelium consists of a few layers of epithelial cells. In proestrum there is rapid growth and the superficial cells become flattened. At heat the epithelium grows until it is 24 cells thick, with several layers of cornified cells. This continues for 3 days after coitus. Toward the end of the period gradual sloughing and leucocytic invasion occurs (3,4). The anestrous smear contains nucleated epithelial cells, which become very numerous in proestrum. The smear of heat contains mostly large, nonnucleated, cornified cells with a few nucleated cells. This is said to be the smear if heat occurs in the spring. Nucleated cells are said to predominate in the smear of a fall heat. During metestrum large numbers of leucocytes appear (11).

UTERUS. In the anestrous uterus the glands are straight and do not extend deeply into the mucosa. Their epithelium is 6 to 12 μ high, and their diameter, 20 to 30 μ. The surface cells are 6 to 12 μ in height. Mitoses are absent. During proestrum the surface epithelium increases to 20 to 24 μ. At heat this layer does not grow further, but the glands almost double in diameter and remain uncoiled. In the lutein phase the epithelial cells revert to their height in anestrum. The glands increase to 120 μ in diameter and the cells to 40 μ. This growth is apparent within 48 hours or less from ovulation and is maintained to from 12 to 15 days, the normal time of implantation. At this time secretion begins in the necks of the glands and proceeds toward the bases, which are actively secreting by the twenty-second day (3). The degree of coiling, also, is very marked. The great glandular growth causes the uterus to resemble that of the rabbit during its lutein phase, but the changes are slower than in that species. If ovulation has not occurred, the uterus retrogresses and there is a marked invasion of leucocytes. The secretory changes in the uterus occur about 3 days earlier in the nonpregnant cat, and, in either case, the collapse of the glands as secretion sets in causes the inner surface of the uterus to become fringed (4).

OVIDUCT. The tubal epithelium during anestrum is 12 to 15 μ high, and cilia are not prominent. In proestrum the calls measure 24 to 40 μ, and cilia are much more prominent. During heat mitoses become appreciable. In the lutein phase the height of the cells decreases, but the extrusion of protoplasm is not so prominent as it is in most other species (3). The cells lose their cilia except in the crypts (4).

The oviduct enters the uterus at its tip on the mesenteric side, then it turns and ends on a low papilla without villi or thickening of the muscle. It is impossible to force fluid from the uterus into the tube (12).

PHYSIOLOGY OF THE FEMALE TRACT

The cat differs from other species with induced ovulation as in this species it can be induced by stimulating the distal portion of the reproductive tract with a glass rod. The interval between stimulation and ovulation is 25 hours or less (2).

If the amount of illumination is increased by exposing cats to longer periods of light beginning in October, they come in heat at the end of November, much earlier than the usual time. It requires about 50 days of treatment to produce an effect (13).

The placenta does not appear to be so good a barrier to hormones as it is in most species since the uterine glands of the newborn kitten are active. This activity ceases soon after birth (14). If the ovaries are removed up to 46 days after coitus, abortion results. If the operation is performed at 49 days or later, the young are carried to term (4).

The removal of one ovary causes a compensatory hypertrophy of the remaining ovary (4).

The uterine muscle has a very low spontaneous motility during anestrum, and the response to drugs at this time is fainter or negative. The muscle always responds to pituitrin. Epinephrin is inhibitory during heat and motor in the lutein phase (3). In the cat ovariectomized for 15 days, the response given is that of relaxation (15). In the pseudopregnant cat the epinephrin reversal response is given from 48 hours after ovulation to 44 days (3).

The anterior pituitary of the mature, anestrous female contains 65 B.U. of lactogen per gram of tissue. During the breeding season this is increased to 224 B.U. (16).

The injection of 100 R.U. of estrogen daily into immature cats, 5 to 13 weeks old (340 to 810 gms.), caused hypertrophy of the vaginal mucosa by

5 days and a little increase in the endometrium. By 9 to 10 days the proestrous type of endometrium had been produced, and by 14 days, the estrous type. These changes could not be hastened by increasing the daily dose to as high as 1,000 R.U. (17). Before nidation pregnancy can very easily be terminated by the injection of estrogens, afterwards a dose of 1,000 R.U. or more, given over 6 days, is needed to produce this result (4).

Heat and ovulation may be induced most effectively during anestrum by injecting F.S.H. together with a very small amount of L.H. The resulting pseudopregnancy lasts 40 to 44 days, judging by the epinephrin reversal test with uterine muscle. This is also the length of normal pseudopregnancy, according to these workers (3). Anestrous cats injected in July were brought in heat by from 22 to 84 R.U. of F.S.H., together with a trace of L.H., given over 6 days. The mean dose for 5 cats was 54 R.U. of F.S.H. Sometimes ovulation and sometimes luteinization of follicles resulted (18). In immature cats the injection of menopause urine at the rate of 20 to 25 R.U. daily causes follicle stimulation. The right ovary tends to respond more than the left, and at this dosage the endometrium is brought into the estrous state (19). In the anestrous cat F.S.H. is more effective in inducing ovulation than is either P.U. or P.M.S., but it is difficult to adjust the dose so that ovulation and pregnancy may occur (20). Gonadotrophic hormones in doses of 50 to 100 M.U. are said to be effective (21).

THE MALE

Early castration inhibits the growth of the penis, and no penial spines are formed (22). The normal male excretes more ketones in the urine than does the female. Castration abolishes this difference, and the injection of testosterone restores it (23).

The lactogen content of the pituitary of the male during the nonbreeding season is 37 B.U. per gm., about two thirds that of the anestrous female (16).

The injection daily of 100 R.U. of estrogen into immature males causes hypertrophy of the glandular epithelium of the prostate (24).

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Felis leo L.

LION

The lion has no fixed breeding season and is polyestrous. Heat may last for a week, and it recurs at intervals of 3 weeks. Two litters may be born in a year. The gestation period is about 108 days (1). Observed gestations have varied from 105 to 113 days. Up to 6 young may be born at a time, but 2 to 3 is the usual number (2).

The anestrous vaginal smear consists of nucleated epithelial cells of various types. During heat it shows mostly large, flat, nonnucleated, cornified cells with a smaller number of cells whose nuclei are pycnotic (3).

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Felis sylvestris Schreber

EUROPEAN WILD CAT

The wild cat in Scotland is apparently seasonally polyestrous, with one heat in the first half of March, a second at the end of May or the beginning of June, and another, rarely, in late fall. Anestrum then sets in until the end of February. The female reaches puberty at less than 12 months (1).

The ovaries are in open capsules. From 2 to 10 follicles rupture at a time, with 5 as the modal number. The corpora lutea are slow to retrogress, and large ones from the first heat persist when mature follicles are present at the second heat. The fertilized ova may transfer from one horn to the other across the body of the uterus (1).

The uterus and vagina are ridged longitudinally. During heat the endometrium has large glands, and at the same time there is extensive desquamation of cornified cells in the vagina (1). Gestation lasts 68 days (2).

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Other FELIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Acinonyx jubatus Schreber South African Cheetah		July to Dec. (Hamilton)	2–4	95 days	Africa
Caracal caracal Schreber Caracal	Probably no fixed season (Shortridge)	Usually July–Aug.	2–4		Africa
Felis bengalensis Kerr Leopard Cat	May (Blanford)		3–4	56 days	S. and E. Asia
F. chaus Güldenstädt Jungle Cat	Two seasons a year (Blanford)		3–4		W. Asia, N. Africa

Other FELIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
F. concolor True Panther, Puma	No fixed season (Hamilton)	Mostly Apr. in N. America	1–4, usually 2; mean 2.4 ± .09	90–93 days	Mountains of N. and S. America
F. glaucula Thomas Long-tailed cat			1		Mexico and Cent. America. One record
F. lybica Forster Gray Wild Cat			2–5, usually 2–3	56 days	Africa
F. lynx L. Lynx	Early May (Elliott)		2–3	63 days	Europe and Asia
F. mearnsi Allen Ocelot			3		Cent. America
F. nigripes Burchell Black-footed Cat			2–3		S. Africa
F. onca True Jaguar		At close of year (Elliott)	2–4	93–110 days	Cent. America
F. pardalis L. Ocelot	End of year to Jan. (Cabrera and Yepes)		2		Cent. and S. America
F. pardus L. Leopard	Breeds all year (Shortridge)	In India, most young born Apr. (Brander)	1–4, usually 3	92–95 days	Asia and Africa
F. ramsayi Miller Jaguar	No definite season (Miller)				Brazil

Other FELIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
F. tigrina Erxleben Margay			2		S. America
F. tigris L. Tiger	No definite season (Blanford)		1–6, usually 2–3	105–109 days	Asia
F. uncia Schreber Ounce, Snow Leopard				93 days	Cent. Asia
Herpailurus yaguarondi Desmarest Jaguar	End of year (Cabrera and Yepes)		2–3	9 months	S. America
Lynx canadensis Kerr Canadian Lynx, Bobcat	First half of March (Seton)		1–4	2 months	N. America
L. rufus Schreber Bobcat	Late Feb. (Hamilton)	Mostly Apr., but may be anytime (Grinnell)	1–4; mean 2.8 ± .2, modes 2 and 4	About 50 days	N. America
Oncifelis geoffroyi D'Orbigny	Once a year (Cabrera and Yepes)		2–3		S. America

PINNIPEDIA

THE seals and walruses breed once a year, in spring soon after they have given birth to their young. This gives a gestation period of almost a year. Delayed implantation has been found in one species and one may guess that it is the rule in most.

OTARIIDAE

Callorhinus ursinus L.

NORTHERN FUR SEAL

The fur seal of Arctic waters has its young from about June 20 to July 20, and mates a few days afterwards (1). The number of young is usually 1. Females approaching their first ovulation have large follicles in only one ovary. In the adult, ovulation and implantation occur in the ovary and uterus which was inactive the previous year. The corpus luteum persists for more than a year. Embryos have not been seen macroscopically in females killed in November; consequently, it is believed that delayed implantation is the rule, especially since blastocysts have been found in July and August (2).

1. Bailey, V. North American Fauna, No. 55, 1936.
2. Enders, R. K., O. P. Pearson, and A. K. Pearson. Anat. Rec., 91: No. 4., proc. 9, 1945.

Other OTARIIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Arctocephalus australis Zimmermann	Atlantic coast, Dec., Jan.; Chilean coast, Nov., Dec. (Cabrera and Yepes)		1	11 months	S. America
A. forsteri Lesson Fur Seal		Nov. 10–Dec. 10 (Shortridge)	1, sometimes 2		Australian coast. Puberty at 3 years
A. pusillus Schreber Cape Fur Seal	Almost immediately after birth of pups (Shortridge)	Nov.–Jan.	1–2, usually 2	11–12 months	S. African coast
Eumetopias jubata Schreber Northern Sea Lion	June, soon after parturition (N.A.F. 55)		1		N. Pacific coast
Otaria flavescens Shaw (Often regarded as a subspecies of *O. jubata*)	Spring	Jan.–Feb. in Argentina; Nov. in Chile (Cabrera and Yepes)	1	About 330 days	S. American coast. Puberty at 2 years in both sexes (Arregni and Regalado)
O. jubata Forster Southern Sea Lion	Summer	Dec.–Jan.			Falkland Is. Puberty at 6 years (J. E. Hamilton)
Zalophus californianus Lesson Californian Sea Lion	June 15–July 15 (Rowley)	June	1	11½ months	California

PHOCIDAE

Leptonychotes weddellii Allen

WEDDELL'S SEAL

Weddell's seal reaches puberty at 2 years of age in the female. In the Bay of Whales, Antarctica, 44 births of known date all occurred between October 5 and November 10; the median date was October 23. The number of young is usually 1, rarely 2, and the period of gestation is long, with 10 months and 10 days as a probable maximum (1).

1. Lindsey, A. A. J. Mammalogy, 18: 127–144, 1937.

Phoca groenlandica Erxleben

GREENLAND SEAL, HARP SEAL

The calving time of the Greenland seal is from the second half of February to the first half of March. A few calve later, the latest observed date being April 15. The last to calve are the young cows with their first calves. The sex ratio in 1,414 calves was 51 per cent males (1). They do not breed until they are 4 years old (2).

1. Dorofejev, S. V. C. R. (Doklady) de l'Acad. de Sci. de l'U.R.S.S. 11: 47–48, 1936.
2. Colman, J. S. J. Anim. Ecol., 6: 145–159, 1937.

Phoca vitulina L.

HARBOR SEAL

On the Pacific coast of North America the harbor seal is born over a period of 3 to 4 months beginning in May. The season is later in inland waters, in Puget Sound, for example. The number of young born is 1, rarely 2. Mating

is believed to be most frequent in September. The age of puberty of the female is at least 2 years. Spermatogenesis begins early in July (1). On the coast of Holland the young are born early in July, and mating is about the beginning of September. The male is believed to reach puberty at the end of its third year, at which time a sudden growth of the baculum occurs (2).

1. Scheffer, V. B., and J. W. Slipp. Am. Midland Nat., 32: 373–416, 1944.
2. Havinga, B. Tijdschr. Ned. dierk. Vereen., Ser. 3, 3: 79–111, 1933.

Other PHOCIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	GESTATION PERIOD	HABITAT, ETC.
Cystophora cristata Erxleben Hooded Seal				N. Atlantic. Puberty at 4 years (Colman)
Mirounga leonina L. Sea Elephant	Oct.–Nov., 20–25 days after parturition (Cabrera and Yepes)		About 340 days	
Phoca hispida Schreber Ringed Seal		Feb.–March (Bailey and Hender)	276 days	Greenland and Labrador

ODOBENIDAE

Odobenus divergens Illiger Pacific Walrus	June to early July (Murie)	May to early June	11 months	Alaska. Puberty: male, 5–6 years; female, 4–5 years
O. rosmarus L. Atlantic Walrus	Mid-April to end May (Capskii)		About 1 year	Puberty: male, 5 years; female, 4 years

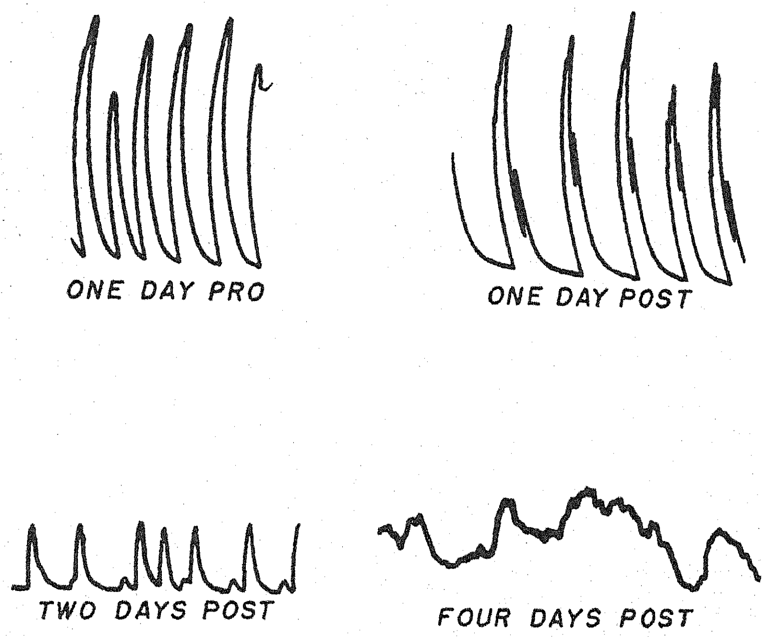

PLATE XI. Contractions of uterine muscle in relation to the estrous cycle in the cow.

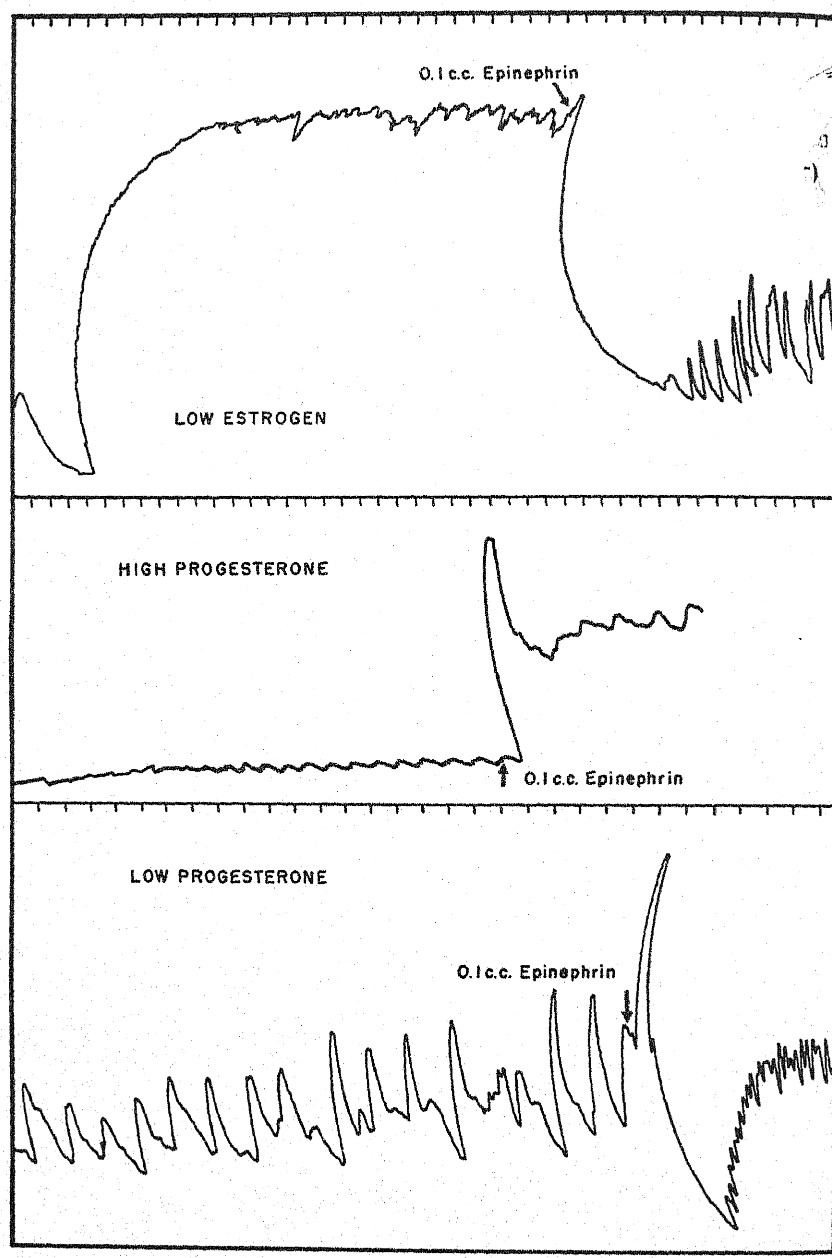

PLATE XII. Epinephrin effects upon uterine muscle when the ovariectomized cow is treated with varying amounts of ovarian hormones. *Top:* Low estrogen, relaxation. *Center:* High progesterone, contraction. *Bottom:* Low estrogen with low progesterone, diphasic effect.

CETACEA

ALTHOUGH our knowledge of the breeding habits of whales is limited, enough is known to question whether, as a rule, there is a definite breeding season. Embryos of various sizes have been found in females at the same time of year. Many species are polyestrous. It is interesting to note the persistence of corpora lutea throughout most of their lives, so that the number found in the ovaries is some indication of the age of the females.

DELPHINIDAE

Delphinus delphis L.

COMMON OCEAN DOLPHIN

The young are still attached to the mother by the umbilical cord several days after parturition. At this time the placentae and corpora lutea are still present, and the latter show no signs of involution (1). The period of gestation is said to be 276 days.

1. Khvatov, V. P. Bul. Biol. Méd. Exp. U.R.S.S., 5: 27–88, 1938.

Other DELPHINIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Delphinapterus leucas Pallas White Whale			1		One record

Other DELPHINIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT ETC.
Globiocephalus scammoni Cope Blackfish		Any time			N. Pacific Ocean
Phocaena phocoena L. Harbor Porpoise	July–Oct. (Calkin)	Apr. to mid-June	1	183 days	N. Atlantic Ocean
P. phocaenoides Cuvier Little Indian Porpoise		Oct.	1		
Pseudorca crassidens Owen False Killer Whale	Polyestrous, except in winter (Comrie and Adam)		1		
Monodon monoceros L. Narwhal	No definite season (Parsild)		1		Arctic seas
Tursiops truncatus Montague Bottlenose Dolphin			1		Atlantic Ocean
Stenella plagiodon Cope Long-snouted Dolphin			1		Atlantic coast of U.S.
Platanista gangetica Lebeck Ganges Dolphin		Apr.–July	1, rarely 2	8–9 months	Indian rivers

INIIDAE

Inia geoffroyensis Gray			1		Amazon River

KOGIIDAE

Kogia breviceps Blainville Pygmy Sperm Whale	Late summer (G. M. Allen)	Spring	1	About 9 months	

PHYSETERIDAE

Physeter catodon L.

SPERM WHALE, CACHALOT

Sperm whales usually mate from August to December, with the peak in October, and calving is from December to April, mostly in February. They breed once in 2 years, and the females are polyestrous. There is no lactation anestrum. The male is fecund all the year round. It reaches puberty before 2 years of age, and the female at about 15 months. Gestation lasts about a year, and 1 young is born at a time (1).

One testis without epididymis weighed 6.38 kg. The internal diameter of the tubules of the tail of the epididymis is 2 mm., and of the vas deferens, 5 mm. The head length of the spermatozoa is $4.93 \pm .017\ \mu$, and the breadth, $2.67 \pm .012\ \mu$. The total length is $40.6\ \mu$ (2).

1. Matthews, L. H. Discovery Reports, 17: 93–168, 1938.
2. Yamam, J. Zeit. Zucht., 34B: 105–109, 1936.

ZIPHIIDAE

Hyperoödon ampullatus Forster

BOTTLENOSE WHALE

The mating time of the bottlenose whale is April and May. In the Arctic the young are born before May and June. The female may be pregnant while lactating. One young is the rule, and the period of gestation is about 12 months (1).

1. Ohlin, A. Lund, Acta Univ., 29: No. 2, 1892–93.

Mesoplodon mirum True

TRUE'S BEAKED WHALE

A single record gives 1 as the number of young born.

BALAENIDAE

SPECIES	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Eubalaena australis Desmoulins Southern Right Whale	June–July (Shortridge)	1		Southern Hemisphere
E. glacialis Borowski Atlantic Right Whale	March (Millais)		276, 360 days	N. Atlantic Ocean

BALAENOPTERIDAE

Balaenoptera borealis Lesson

LESSER RORQUAL, SEI WHALE

The lesser rorqual breeds at the age of 2 years. The female is polyestrous and the season is from May to August, with its maximum in July. There is an anestrous period of 6 to 7 months from the end of lactation to the beginning of the next pregnancy. Gestation lasts about 12 months. The male is fecund all the year round (1,2). Breeding occurs in tropical and subtropical waters (3).

1. Matthews, L. H. Discovery Reports, 17: 183–290, 1938.
2. Zenkovič, B. A. Dokl. Akad. Nauk, S.S.S.R., 2: 337–343, 1935.
3. Kellogg, R. National Geographic Mag., 77: 35–90, 1940.

Balaenoptera physalus L.

FINNER WHALE

The finner whale reaches puberty at the age of 2 years, and matings occur during the months from November to March (1). The corpora lutea persist throughout life in a more or less degenerated condition (2). The duration of gestation has been given by various authorities as between 305 and 365 days.

1. Zenkovič, B. A. Dokl. Akad. Nauk, S.S.S.R., 2: 337–343, 1935.
2. Peters, N. Zool. Anz., 127: 193–204, 1939.

Megaptera novaeangliae Borowski

HUMPBACKED WHALE

This whale, also described as *M. nodosa* and by other names, mates in the Southern Hemisphere from August to November, mostly in September, and most births are from July to September. The female is polyestrous and usually breeds once in 2 years, occasionally twice in 3 years. The gestation period is about 11 months (1). Other records of births are so varied that it may be doubted whether there is any regular breeding season, or possibly mating and calving grounds are often scattered climatically. The usual number of young is 1, but twins are common (2).

1. Matthews, L. H. Discovery Reports, 17: 8–92, 1938.
2. Cabrera, A., and J. Yepes. Historia Natural Ediar. Mamiferos Sud Americanos. Buenos Aires, 1940.

Sibbaldus musculus L.

BLUE WHALE

Puberty is reached when the blue whale is 2 years old (1). There is said to be no regular breeding season, and gestation lasts about 1 year (2). Single

births are the rule, but twins are not uncommon (3). The ovary weighs 4 to 5 kg., and it contains about 500 cc. of liquor folliculi which has an estrogen value of about 2,000 M.U. per liter. The corpus luteum may weigh 4 kg., and, after preservation in a frozen state for a year, the tissue gave a progesterone value of 60 Rab.U. per kg. The anterior pituitary weighs 30 g. (4). The corpus luteum remains throughout life in a more or less degenerated state (5).

1. Krogh, A. Nature, 133: 635–637, 1934.
2. Lillie, D. G. Proc. Zool. Soc., London, 769–792, 1910.
3. Bailey, V. North American Fauna, No. 55, 1936.
4. Jacobsen, A. P. Nature, 136: 1029, 1935.
5. Peters, N. Zool. Anz., 127: 193–204, 1939.

RHACHIANECTIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG
Rhachianectes glaucus Cope Gray Whale	April (N.A.F. 55)	Last half of Jan. (Kellogg)	1

NOMARTHRA

MANIDAE

SPECIES	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Manis pentadactyla L. Indian Pangolin	Jan.–March in Deccan, July in Shevroy Hills (Blanford)	1, rarely 2	India
Smutsia temminckii Smuts Scaly Anteater		1	S. Africa

XENARTHRA

DELAYED implantation of the embryos is probably common in the Xenarthra, and in this connection it is interesting to note that the activity of the corpus luteum is believed to be in abeyance until implantation occurs. Lactogen assays of the anterior pituitary might reveal data of interest in this respect. Polyembryony is also common in the order.

BRADYPODIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Bradypus cuculliger Wagler Three-toed Sloth	March–April (Beebee)	July–Sept., mostly Aug.	1		S. America
B. griseus Gray Gray Sloth	Possibly Dec. in Panama (Enders). Probably all year, mostly early in dry season (Britton)			4–6 months	Cent. and S. America

MYRMECOPHAGIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Cyclopes dorsalis Gray Anteater	Dec., Jan. in Panama (Enders)	1		Cent. and S. America
Myrmecophaga tridactyla L. Giant Anteater		1	190 days	S. America

DASYPODIDAE

Dasypus hybridus Desmarest

MULITA ARMADILLO

It is believed that this armadillo, like *D. novemcinctus,* has a gestation period which is prolonged by delayed implantation. In Argentina implantation occurs about June 1, and birth is in October. The embryos are free for at least two months. Polyembryony is the rule, as many as twelve identical twins being produced from one ovum (1,2).

1. Fernandez, M. Morphol. Jahrb., 39: 302–333, 1909.
2. Hamlett, G. W. D. Quart. Rev. Biol., 10: 432–447, 1935.

Dasypus novemcinctus L.

NINE-BANDED ARMADILLO

This armadillo of southern North America and Central America breeds in Texas in July. The cells of the corpus luteum appear to be inactive until implantation, when secretory droplets appear. Its removal after this time is

followed by abortion or resorption of the embryos (1). Implantation is delayed at least 3 weeks (2). The fertilized egg divides and the segments separate so that at least 4 identical embryos are produced (polyembryony). Implantation occurs in November and birth early in March (1).

1. Hamlett, G. W. D. Quart. Rev. Biol., 10: 432–447, 1935.
2. Patterson, J. T. J. Morphol., 24: 559–684, 1913.

Other DASYPODIDAE

SPECIES	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Giebel *Euphractus villosus* Hairy Armadillo		65 days	S. America
Tolypeutes tricinctus L. Three-banded Armadillo	1		S. America

TUBULIDENTATA

ORYCTEROPODIDAE

Orycteropus afer Pallas

AARDVARK

THE aardvark or ant bear, which inhabits Africa, gives birth to its young during the months from May to July (1).

1. FitzSimons, F. W. The Natural History of South Africa. London, 1919.

LAGOMORPHA

OUR knowledge of reproduction in the Order Lagomorpha is practically confined to the domestic rabbit; hence it is not possible to make generalizations.

OCHOTONIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Ochotona daurica Pallas Dahurian Pika	Two litters a year (Loukashkin)			Manchuria
O. princeps Richardson Brown Pika	Possibly 2 litters a year (Wallace)	Summer	2–3, usually 3	Northern Rocky Mountains
O. schisticeps Merriam Mountain Cony			3–4	Western U.S.

LEPORIDAE

Lepus americanus Erxleben

SNOWSHOE HARE

The snowshoe rabbit or hare of North America mates first in March. In Manitoba it continues breeding until early June (1), but further south it may continue to breed until August (2). It is polyestrous and reaches puberty during the second year of life. The litter varies from 1 to 7, with a mean size of 2.8, and a mode at 3 (3), but it may have 8 to 10 young in years of plague (1). There is a postparturient heat (4).

The vulva is swollen and red when the female is in heat; the first litter is born in April, the maximum number of litters are born in May, and the season declines in June and July. The gestation period is 38 days. The mating season is advanced by at least 30 days if the hares are exposed to 18 hours of light a day in winter. Masking the eyes prevents this effect, and transfer from 18 to 9 hours of light causes the developing gonads to regress (5).

When the hare is brown in color there is a large amount of gonadotrophic hormones in the blood; when it is white the level is low. The injection of gonadotrophic hormones into physiologically white animals caused the hair to become much darker and provoked a copious shedding of the winter hair (5).

In January the testes are small and abdominal. They increase in size during February and descend near the end of the month. They reach their maximum weight in March and rapidly decrease from July onwards. In September their weight is lowest and they return to the abdomen. The penis is pale, almost white, in the nonbreeding season. Just before the breeding season it becomes red at the tip, and the color soon spreads to the whole penis. This organ is pale throughout the first year of life, and the males do not mate until their second year (3). Reduction of the amount of light delays testis growth in the spring (5).

1. Seton, E. T. Life Histories of North American Animals. New York, 1909.
2. Hamilton, W. J., Jr. The Mammals of Eastern United States. Ithaca, 1943.
3. Aldous, C. M. J. Mammalogy, 18: 46–57, 1937.
4. Severaid, J. H. The Snowshoe Hare, Its Life History and Artificial Propagation. Augusta, Me., 1942.
5. Lyman, C. P. Bul. Museum Comp. Zool., Harvard College, 93: 393–461, 1943.

Lepus europaeus Pallas

COMMON HARE

On the Ciscaucasian steppes the breeding season of the European hare lasts from mid-winter until the middle of summer, when drought causes its cessation. The average embryo number and litter size in relation to the seasons are given as follows (1):

	Embryos	Litter size
Winter	1.7	1.5
Spring	3.5	3.3
Summer	3.7	3.1
Autumn	3.0	2.0

In England breeding begins in November or December, is at a maximum in March, and virtually ceases in July, but litters have been found at all times of the year (2). The duration of gestation is given as 30 to 42 days (1).

1. Kolosov, A. M. Zool. Ž. (Mosk.), 20: 154–172, 1941.
2. Barrett-Hamilton, G. E. H. A History of British Mammals. London, 1910.

Oryctolagus cuniculus L.

DOMESTIC RABBIT

The rabbit will breed more or less at any time of the year but there are no cycles. The female ovulates only after coitus or under strong sexual excitement. The usual interval between stimulation and ovulation is 10 hours, and during the first hour of this period sufficient F.S.H. is released from the pituitary to cause the preovulatory ripening of the graafian follicles. Follicles reach the estrous stage in waves, and the female may remain in heat for a month or more at a time in the absence of the male. If coitus does not result in pregnancy, which lasts for 30 to 32 days, corpora lutea are formed which last for about 16 days. At the end of this time the doe makes a nest by plucking fur from her breast, and her mammary glands are in condition

for lactation, just as if she were pregnant. This condition is called pseudopregnancy. During the lutein phase glandular development in the uterine mucosa is very great, so that a transverse section appears like open lacework. The vaginal smear is not a reliable indication of the reproductive state.

REPRODUCTION IN GENERAL

The age of puberty in rabbits is affected by breed differences, but there is very little information on this point. It is also affected by the time of birth. Does born in the fall reach puberty (fertility) in about 5½ months, but those born in the spring require about 8½ months. They tend to copulate 1 to 2 months before they are capable of ovulation. In England, does kept in unheated rooms often experience anestrum from October to March, but the tendency is not absolute. The optimum season for reproduction is from May to July (1). In the United States it has been the writer's experience that July to September, when the temperature is high, are the poorest months. As does pass into the anestrous condition, copulation may occur but graafian follicles do not reach the state at which they are capable of rupturing (1). During the breeding season, in the absence of the male, the doe remains in heat almost indefinitely, and during this time waves of follicles mature, last for about 7 to 10 days, and then become atretic (2). If does are kept in continuous light or in total darkness, this rhythm of growth is not affected except that more large follicles are present in the does kept in the light (3). Atresia may be due to degeneration and phagocytosis of the granulosa, with fibrotic ingrowth of the theca interna, or to extravasation of blood and the formation of blood follicles (4). If coitus is permitted, the mature follicles begin to grow by copious secretion of liquor folliculi, and rupture occurs about 10 hours afterward (5).

The stimulus for this growth is apparently emotional since intense excitement, such as the act of mounting or being mounted by another doe, evokes it and since local anesthesia of the vagina and vulva just before coitus does not prevent its occurrence (6). It is due to the release of a gonadotrophic hormone from the anterior pituitary since removal of that organ within an hour post coitum prevents ovulation. If the operation is performed after that time, ovulation occurs as usual and corpora lutea are formed. Evidently the pituitary releases sufficient hormone in a little more than an hour after coitus (7,8). The pituitary may also be caused to release the stimulating hormones by electrical stimulation of the head or of the lumbar region of the

cord, but the action is somewhat slower (9); by the intravenous injection of 0.9 to 1.1 mg. of picrotoxin (a hypothalamic stimulant) per kg. of body weight (10); and by salts of copper and cadmium (11). This stimulus is necessary for the formation of corpora lutea since rupture of mature follicles by pricking is ineffective (12,13).

The ovaries produce corpora lutea with approximately equal frequency; a series of records gave 51.4 per cent of corpora lutea in the left ovary (1).

The fact that ovulation usually occurs only after coitus enabled the pioneer worker to differentiate clearly between the estrogen and lutein phases of the cycle. Pseudopregnancy, the condition when sterile coitus, the injection of gonadotrophes, or the use of one of the methods described above, has caused ovulation and corpus luteum development, lasts normally for 16 to 17 days (1,14). But pseudopregnancy in the doe whose uteri have been removed lasts from 24 to 29 days (15). The corpora lutea of the cycle in the guinea pig similarly treated remain for a much longer period, but those of the rat are not prolonged. It is an open question whether removal of the uterus removes an impulse which normally brings an end to the life of the corpus luteum (in contrast to the action during pregnancy), or whether this organ uses a substance needed by the corpus luteum. More work is needed on the problem.

The doe rabbit matures follicles and is ready to ovulate immediately after the end of pregnancy or of pseudopregnancy (1).

In order to test the length of life of the ovum by artificial insemination at different times, it is necessary to arrange that eggs shall be shed. Thus, in such an experiment, sterile coitus with a vasectomized buck is allowed with the knowledge that ovulation will occur about 10 hours later. This is a great advantage in work of this nature, and also in obtaining dated material for embryological work. The time of ovulation in the rabbit can be obtained with greater accuracy than is possible in any other species. It has been found that, after allowing for the time taken by the spermatozoa to reach the top of the oviduct, the eggs have a fertile life of not more than 6 hours after ovulation. They are capable of being fertilized only while they are in, or as they leave, the plug of extruded liquor folliculi at the top of the oviduct. As they move down the tube and acquire a layer of albumin, they can no longer be fertilized. The percentage of successful inseminations and the litter size decrease at a constant rate with inseminations from 5 hours before to 2 hours after ovulation (16).

Ova just liberated from the follicles are surrounded by cumulus cells of

the stratum granulosa. If spermatozoa are present, these cells are dispersed by the first ones to penetrate into the mass. This happens normally within 1 to 1½ hours after ovulation. If spermatozoa are not present, it takes about 17 hours for the separation to occur. The passage through the oviduct takes about 62 to 82 hours (17).

The litter size of rabbits varies with the strain or breed. Thus, a fecund inbred strain has given a mean litter size of $8.1 \pm .2$, with a mode of 9, a range of 1 to 13, and a standard deviation of 2.7; but a strain of small (Polish) rabbits gave as mean $4.0 \pm .1$, mode 4, range 1 to 7, and standard deviation, 1.54. About 20 per cent of the eggs shed fail to develop to term. This is partly due to loss of ova and partly to fetal atrophy (16). The latter is caused in large measure by inherited factors acting through the mother (18). The mean litter size rises until the doe is at least 3 years old (19). Experimentally it is reduced if artificial insemination is performed 24 or more hours before (20), or fewer than 5 hours before, ovulation. In the first case too few spermatozoa survive, and in the second case too few eggs (16). The sex ratio is 53.1 per cent males (21).

The duration of gestation is usually 30 to 32 days. An extensive series gave $31.08 \pm .02$ days, standard deviation, 0.83 days; and mode, 31 days (22). It is affected by breed: Polish rabbits had a mean gestation of 30.4 days and an inbred albino strain, 32.9 days. It does not vary with the season or the age of the mother (23) but tends to be higher within the breed when small litters are carried (24). The same is true if the smaller litter is experimentally produced (25).

In a doe which is allowed to become pregnant immediately after parturition and which is suckling a large litter, above 3 to 4, implantation is not delayed but the embryos die in the blastocyst stage. If smaller litters are suckled, the pregnancy continues and lasts the usual time. A suckling doe goes out of heat in about a week because of follicular atresia and the loss of about half the normal weight of the ovaries. The uteri also atrophy and almost resemble the state found in an ovariectomized doe. New follicles mature rapidly after weaning (1).

HISTOLOGY OF THE FEMALE TRACT

OVARY. Soon after birth the nests of cells which include the germ cells tend to atrophy. They are largely replaced by the production of epithelial invaginations, which begin at about 35 days of age, are at their maximum

from 51 to 60 days, and then fall off (26). It is said by some that there are further waves of ovogenesis at 8 and 14 months and that at these times the amount of interstitial tissue diminishes (27), but these waves are probably not so intense as the earlier ones, since others have found little neogenesis of ova in mature rabbits. According to the latter workers, atresia of oöcytes is small, only 10 per cent at any time, although in larger follicles it amounts to 60 per cent (28).

As ovulation can be so easily timed, it has been observed and photographed on numerous occasions. The diameter of the mature follicle at coitus is about 1.5 mm. It is relatively flat and has a bluish tinge. Most growth occurs between 3 and 6 hours after coitus, and the follicle protrudes slightly from the surface of the ovary. At 9 hours the vascularity of the theca increases, and there is some slight hypertrophy of the epithelial cells of the theca interna. The first sign of approaching ovulation is the gradual formation of the macula pellucida, a small clear area projecting from the follicle and surrounded by a network of capillaries. As the macula increases in height the blood vessels rupture, and a small blood clot forms below the ultimate point of opening. At this time the follicle is about 1.8 mm. in diameter. Rupture and extrusion of liquor folliculi and the ovum through a small opening at the apex take about 7 seconds. The liquor folliculi does not flow much but forms a small cone. The greater part of it remains in the cavity, which does not collapse to any great extent. Later, the floor of the follicle approaches the surface so that the corpus luteum, with the point, which becomes luteinized, projects from the surface of the ovary more than the follicle from which it was derived (13,29).

In the ruptured follicle the granulosa cells are nearly all retained, but there is rarely any blood clot except near the point of rupture. Hypertrophy of these cells and ingrowth of the theca interna begin immediately. By 6 hours the ingrowth of connective tissue in the form of spindle-shaped theca cells is marked, and by the fourth day the central cavity, filled with liquor folliculi, has been almost entirely obliterated. By 8 days the lutein cells reach their full development, and are about eight times their former diameter. The corpora lutea of pregnancy persist throughout gestation and are reabsorbed gradually after its termination, but somewhat more rapidly if the doe is lactating. Those of pseudopregnancy begin to degenerate at 18 days. A visible sign of degeneration is an abrupt change from a pinkish vascular state to a chalky yellow avascular one (1,30).

The size of the ovum is 123.0 $\pm$ 1.9 μ without, or 188.6 $\pm$ 2.0 μ with, the zona pellucida (31), a comparatively large size for mammals.

VAGINA. The vulva of the rabbit in heat is usually purple to reddish pink and somewhat swollen. This is a good, but not infallible, sign of heat since at other times it is pale. The vaginal epithelium is more or less stratified, with many mucous cells, especially near the cervices, and it does not undergo characteristic changes with heat. Similarly, smears are not reliable as indications of the reproductive state (32,33), a fact which is common in those species in which mucous cells are frequent.

UTERUS. The cervices are not plugged at any time by a seal of mucus. The endometrium is very vascular during the follicular phase, but the glands are not much developed. In the lutein, or progestational, phase the glands undergo marked development. The lumens are much expanded, with the result that the appearance resembles that of open lace. During the stage of involution, when the corpora lutea are retrogressing, extensive extravasation of blood has been described (34). The uterus is ciliated in a zone extending from 1.5 cm. from the os uteri anteriorly. In the region of the cervix ciliation is abundant, but this type of epithelium is scanty elsewhere until the tubo-uterine junction is reached. Ciliated cells do not vary in number with the physiological state of the animal (35). The uterine epithelium is said to become a syncytium during the life of the corpus luteum (36).

The oviduct is ciliated, the tubo-uterine junction has four primary folds which project into the uterus, and the muscle forms a slight sphincter. These folds are devoid of glands. According to one account it is difficult to force fluid from the uterus into the oviduct (37), but another worker found it fairly easy (35). Possibly the stage of the "cycle" influences the ease of passage; further work is needed to decide the question.

PHYSIOLOGY OF THE FEMALE TRACT

The corpora lutea are essential for the maintenance of pregnancy. Early removal by ovariectomy causes reabsorption of the embryos; later, abortion is the rule (1,38). It is easy to shell out the corpora lutea, and the question arises, How many are needed to maintain pregnancy, and what is their output of progesterone? The first question has not yet been answered directly. A summary of available information suggests that one corpus luteum is necessary to bring about progestational proliferation (the lacelike condition

of the glands in the uterus), and, as 0.2 mg. daily of progesterone produces the same effect in the ovariectomized rabbit, this must be approximately the daily output of a corpus luteum (39). It has also been shown that to prolong the proliferation for longer than 5 days, more than two corpora lutea are necessary, and to sensitize the uterus sufficiently to produce deciduomata, at least four are necessary (40). As 0.5 to 1.0 mg. of progesterone are needed to maintain pregnancy, these figures tally very well (39), though it must be remembered that smaller litters with fewer corpora lutea are successfully brought to term in the normal female.

Relaxin can be detected in the blood serum as early as 3 days after coitus. It increases rapidly from the twelfth to the twenty-fourth day, when it remains constant for the remainder of pregnancy. It declines rapidly at parturition and has practically disappeared within 3 days. At its maximum, 1 G.P. unit is present in 0.1 cc. of serum. It can also be detected in increasing amounts in the urine throughout gestation (41).

The uterine muscle gives strong, but irregular, contractions when the doe is in heat. At 22 hours after ovulation these contractions change rather abruptly to small irregular ones, and, instead of being sensitive to pituitrin, the muscle becomes insensitive (42). Removal of the corpora lutea quickly restores the sensitivity (43).

The pituitaries of 10-day-old rabbits contain no gonadotrophic hormone, but at 15 and 21 days follicle-stimulating hormone can be detected. At 28 days luteinizer also is present (4). In view of the fact that coitus causes the release of hormones from the pituitary and the ripening of follicles, the content of gonadotrophic hormone before and after coitus has attracted much attention. Before coitus the rabbit's pituitary contains about 30 ovulating units per gland. Half an hour after coitus this has dropped 80 per cent, and after 24 hours it has risen to 1.5 to 5 units (45,46). The ovulating unit used here is the amount required to ovulate a rabbit per kg. body weight. Some authors have used this term for the amount required to cause ovulation in a rabbit weighing about 3 kg. After ovulation the content rises rapidly during pseudopregnancy, reaching a maximum of 60 units at 10 days and falling to 15 at the end. The curve during pregnancy is similar, but the peak is reached at 16 days, and the minimum at 25 days (45). The maximum during pseudopregnancy varies with the season; it is low in fall and winter and high in the spring (46). After mating there is a general reduction of the level of hormones in the pituitary, F.S.H., L.H., thyrotrophic, and adrenotrophic (47), but lactogenic hormone does not change (48). Occasionally a pseudopregnant

rabbit will copulate. When this occurs ovulation does not follow and the pituitary does not lose gonadotrophic hormone (49). The number of granulated acidophils and basophils in the pituitary is greatest during heat. It falls rapidly after coitus, the basophilic degranulation being greatest, and then rises parallel with the gonadotrophic hormone content (50). Removal of the gonads increases the potency of the pituitary, and the effect is more marked in the female than in the male. The potency in the female increases 100 per cent in 3 months, and it is accompanied by a strikingly increased basophilia (51). However, another investigation did not record such a great increase in potency (52).

The estrous rabbit excretes about 5 R.U. of estrogen per liter of urine. Excretion rises to a maximum of 25 R.U. at 11 to 15 days during pseudopregnancy. In pregnancy the level at this time is 100 R.U. and a maximum of 180 R.U. is reached at 16 to 20 days, after which the amount declines rapidly to 10 R.U. at term (53).

The prolactin content of the pituitary of immature females is 140 B.U. per gram of tissue; in the mature female it rises to 420 B.U. (54). In pseudopregnant rabbits it rises to a peak at 5 days, and if the does are suckling the level is 66 per cent higher than if they are not suckling (55).

Immature 4-week-old rabbits do not give an ovarian response to pituitary hormones (56). In adult rabbits the minimal ovulating dose of anterior pituitary extract is 0.1 R.U., and of prolan, 2.0 R.U., but in the rabbit hypophysectomized immediately before injection 25 per cent and 50 per cent more were needed, respectively. The latter figures should approximate the minimum amount released from the pituitary after coitus (57). Another report gives 5 M.U. of prolan as the optimal ovulating dose in the intact animal (58). During pregnancy 10 R.U. of prolan are needed to cause ovulation. If the injection is made at 11 days, there is no interruption of pregnancy, but at 17 days all gestations are interrupted (59). By the injection of prolan (60) or anterior pituitary extracts (61,62) toward the end of pseudopregnancy, this condition can be greatly prolonged if the injections are properly spaced, since new waves of corpora lutea are developed.

In the mature rabbit superovulation is not produced by the injection of P.M.S., probably because the latter causes the immediate rupture of those follicles which are already mature and the luteinization of others (63). Superovulation may be caused in both juvenile and adult does with F.S.H. prepared by tryptic digestion of anterior pituitary extracts. The number of embryos may thus be greatly increased, but few of them survive, with the

result that the number alive in late pregnancy is less than usual (64). The use of horse pituitary extract, which is very high in F.S.H., has produced similar results (65).

Ovulation after electrical stimulation through the head may be inhibited by the injection of 0.5 mg. of estradiol benzoate or 10 mg. of testosterone propionate (66). The injection of 150 R.U. of estrogen daily at 3 to 4 days after coitus prevents implantation, although if the injections are delayed to 5 to 6 days, it is not prevented. Smaller doses at 3 to 4 days reduced the number of implantations (67). The activity of the corpus luteum in producing glandular hypertrophy is inhibited by the injection of 600 I.U. of estrogen; 360 I.U. prevent nidation of the ova, but at 5 to 6 days 720 I.U. are needed to terminate the pregnancy. From 12 days on, 240 I.U. cause abortion (68). If the injection of estrogens is performed within the first 5 days of pseudopregnancy 1,000 R.U. are needed to terminate this condition, and, since 675 R.U. suppress the progestational activity of 3 Rab.U. of progesterone, it may be concluded that the rabbit produces more than 3 Rab.U. of progesterone in the first 5 days of pseudopregnancy (69).

Uterine motility in the doe in heat is rapidly inhibited by the injection of progesterone. It ceases in 4 hours with 0.3 Rab.U., in 2 hours with 0.6 Rab.U., and in 55 minutes with 1.2 Rab.U. (70). On the other hand the muscle in the ovariectomized doe is quiescent by 2 to 3 days after operation. The injection of 2 to 5 R.U. of estrogen per kg. of body weight restores the motility within 24 hours, but during pseudopregnancy 1,090 R.U. per kg. are ineffective (71). This response to estrogen can first be observed 10 hours after the injections are made, and the metabolic rate of the tissue rises with the restoration of motility. Hyperemia of the vascular bed was maximal within 30 minutes of injection (72). With the lack of response to pituitrin as a criterion of progesterone activity it was found that 5 Rab.U. gave complete inhibition in all cases, whereas less than 1 Rab.U. never gave complete inhibition. Above this minimum the number of rabbits which failed to respond to pituitrin gradually increased (73).

The pseudopregnant uterine proliferation is maintained by 0.2 to 0.4 Rab.U. of progesterone daily for the first 6 days, after that 1.5 Rab.U. are required daily to 11 days. After this time increased dosages did not maintain the proliferation, but if 20 R.U. of estrogen were also injected it was maintained. It was also found that in the normal animal the injection of estrogens will maintain the pseudopregnant corpora lutea for longer than the usual 16 days (69). This work has led to the view that the corpus luteum

needs estrogen for its maintenance. It has been found that 1 μg. of estradiol will maintain luteal function in rabbits (74), and that, after removal of the gravid horn in unilaterally pregnant rabbits, 3 μg. of estradiol benzoate a day prevent the involution of the corpora lutea, even beyond the usual term (75). This reaction does not depend on the pituitary since almost similar doses are effective in the hypophysectomized rabbit (76). It is believed, also, that one of the functions of the uterus is to produce estrogens, which maintain the corpora lutea during the second half of pregnancy. After hysterectomy in the first half of this period, they last for the usual pseudopregnant time; but if the operation is performed in the second half they decline precipitously, though they are preserved if estrogens are injected (77).

The blood supply to the uterus is believed to depend to some extent upon the acetyl-choline content of the tissue. It rises in the uteri of spayed does treated with estrogens, but the rise is transient, lasting only 6 hours or less (78).

The injection of large amounts of estrogen causes the tube-locking of ova, a condition which also occurs under similar circumstances in the rat. On the other hand, the injection of progesterone hastens their passage (79). Our knowledge of tubal motility leaves a good deal to be desired.

Certain data upon the effects of progesterone upon the uterus were given in the discussion of the output of the corpus luteum. However, it is known that estrogen is equally necessary, as the following results show: A dose of 0.5 mg. of progesterone twice daily is necessary for implantation after ovariectomy; after 11 days 1.0 mg. twice daily will carry the pregnancy to term (80). According to another account 2.0 I.U. daily are needed from 11 to 15 days, and after that 4.0 I.U. (81), or 5.0 mg. (82); but if a trace (1:1,600) of estrone is added, only 0.5 mg. is needed (83).

Parturition is delayed if a new set of corpora lutea is caused to develop late in pregnancy by the injection of gonadotrophic hormones. The injection of 1.5 I.U. of progesterone daily at, and after, the normal time of parturition has the same effect. The fetuses continue to grow but do not live beyond the thirty-fifth day *in utero*. Parturition usually becomes abnormal (84). The injection of estrogens at the rate of 150 I.U. daily toward the end of pregnancy also maintains the corpora lutea and produces the same effect, but if the doe has been ovariectomized parturition follows despite the injections (85).

In the hypophysectomized rabbit it has been found that injected progesterone and estrogens have the usual effects upon the endometrium, but the effect is not so great as in the ovariectomized, injected rabbit whose pituitary is intact (86). The same results were obtained with estrogen alone

(87) and with progesterone alone (88), although it has also been found that a greater amount of progesterone is needed under these conditions to produce a given effect (89). Pregnancy may also be prolonged in the hypophysectomized rabbit by the combined injection of 1.9 to 2.5 mg. of progesterone and 2 μg. of estradiol benzoate daily (90).

The pH of fluids secreted in isolated segments of the uteri of rabbits brought into heat by the injection of stilbestrol averaged 7.8, with a range from 7.73 to 7.90 (91).

The dewlap is apparently a secondary sexual character in rabbits as it is rarely present in the males, but usually present in the females, of certain breeds. Its development may be inhibited or its involution may be caused by ovariectomy. In males its development may be induced by the injection of estrogens (92).

THE MALE

The average ejaculate of the buck rabbit is 0.32 cc. with 200,000,000 spermatozoa per cc. (93). If fewer than 1,000,000 spermatozoa are used at a time in artificial insemination, the chance of fertilization is reduced, but if the number used is below 10,000, fertilization does not occur at all (94). The mean pH of the semen is 7.20 (95).

There is no compensatory hypertrophy of the testis after unilateral castration, and the number of spermatozoa is related to the testis weight. Thus, in the animal with one testis only half the usual number of spermatozoa are produced (96).

The spermatozoa pass through the epididymis in 4 to 7 days (96). No vaginal plug is formed at copulation. The spermatozoa find their way into the uterus by penetration, not by suction or peristalsis (97), but they are transported up the uterus to the tubo-uterine junction in a short while, less than 5 minutes (98), and this is said to involve peristaltic action (99).

The amount of testosterone needed to cause a buck castrated early in life to copulate is 10 mg. per day (100).

The normal male pituitary contains more gonadotrophic hormones than that of the female; after castration the potency increases 36 per cent in 3 months, in contrast to the 100 per cent increase recorded for the female (51). The pituitary of the normal male is higher than that of the female in both F.S.H. and L.H. content. At 10 days of age there is no gonadotrophic hormone at all. At 15 to 21 days there is follicle stimulator only, although from 25

days onward both hormones are present (44). The prolactin content of the pituitary is increased if estrogen is injected into males, but 5,000 I.U. injected over a period of 10 days is less effective than 500 or 1,000 I.U. (101).

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Sylvilagus floridanus Allen

EASTERN COTTONTAIL RABBIT

This rabbit, which lives in North America east of the Rocky Mountains, is polyestrous and breeds from mid-January into August, though the season may be curtailed for a month at either end in the northern part of its range. The young reach puberty at 40 weeks, and in the breeding season several litters are produced (1). The average litter size is 4.5 (2); or 5.0 ± .13, with a range from 2 to 7, and a mode of 4 to 5 (3). The gestation period has been observed as 26.5 days (4), but is usually given as 30 days (1).

The testes enlarge late in December and soon descend. They remain in the scrotum until September, at which time they still contain spermatozoa (1).

The level of gonadotrophic hormones in the pituitary of the male is at a minimum from October to January and at a maximum in March, when it is 600 per cent of the minimal level. There is a rapid decrease in early fall.

The percentage of basophils rises from 4.4 to 13.8 during the transition from the nonbreeding to the breeding state. The weights of the testes, seminal vesicles, and prostate make corresponding changes. In the female there are no significant seasonal changes in the gonadotrophe level or in basophil numbers (5).

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Sylvilagus transitionalis Bangs

NEW ENGLAND COTTONTAIL

This cottontail of the eastern United States has a limited breeding season beginning in mid-April. It has 3 to 4 litters a year. When these rabbits were treated with artificial light at night, beginning in December, increased sexual activity was observed in January, 23 days later (1).

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Other LEPORIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Brachylagus idahoensis Merriam Pygmy Rabbit	Probably 2 litters a year (N.A.F. 55)		5–8		Idaho, California, Oregon, Nevada
Lepus alleni Mearns			Av. 1.93		Southwestern N. America
L. arcticus Ross Arctic hare	Early May (Howell)		4–8, usually 6–8		Hudson Bay, Labrador, Newfoundland
L. bairdii Hayden	Late spring, early summer (Warren)		2–6		Rocky Mountains

Other LEPORIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
L. californicus Gray Californian Jack Rabbit	Several litters a year (N.A.F. 55)	Apr.–Aug.	1–7, av. 4.1		Western N. America
L. campestris Bachman White-tailed Jack Rabbit	April (Seton)	June to early July	3–6, usually 4		Western N. America
L. capensis L. Cape Hare	Wet season, polyestrous (Fitzsimons)		2–5, usually 2		Cent. and S. Africa
L. hibernicus Bell Irish Hare	All year (Barrett-Hamilton)	Mostly March	2–6, usually 3		Ireland
L. nigricollis Cuvier Black-naped Hare	Oct.–Feb. (Blanford)		1–2, usually 1		India
L. ruficaudatus Geoffroy Common Indian Hare			1–2		India
L. saxatilis Cuvier Mountain Hare	Polyestrous, Oct.–Apr. (Fitzsimons)		2–5, usually 2	About 1 month	Cent. and S. Africa
L. variabilis Pallas Varying Hare	Cycles about 2 months (Heape). Feb. onwards (Barrett-Hamilton)		1–8		Northern Europe
Pronolagus crassicaudatus Geoffroy Red Rock Hare		Pregnant Jan. (Roberts)	1–2		Cent. and S. Africa
Sylvilagus aquaticus Bachman Swamp Rabbit	Two litters a year (Hamilton)		1–6		South Central U.S.

Other LEPORIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
S. audubonii Baird	All year, mostly June–Oct. (Ingles; N.A.F. 53)		2	28–30 days	Western N. America
S. gabbei Allen			4		Cent. America
S. nuttalli Bachman Oregon Cottontail Rabbit		Apr.–July (N.A.F. 55)	3–6		Northwestern U.S.
S. palustris Bachman Marsh Rabbit	Early Feb., Oct., or longer (Hamilton; Tompkins)		2–5		Southeastern U.S.

LAGOMYIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Lagomys roylei Ogilby Himalayan Mouse Hare			4		India, 1 record

RODENTIA

THE rodents comprise a large number of species, and their habits are so diverse that it is not surprising to find a variety of reproductive patterns among them. In many cases it is very difficult to observe their reproduction owing to their nocturnal or subterranean habits.

In the Sciuridae probably most species are polyestrous during the spring and summer, with an anestrous period during hibernation. One species, the thirteen-lined ground squirrel, is known to ovulate only after coitus, and probably many others have the same habit. Apparently there is no heat or ovulation until lactation is finished, and this reduces the possible annual number of litters.

The Geomyidae seem to have a bewildering variety of patterns, even in one genus. Some seem to be polyestrous all the year, some are for a limited period, and some are said to have only one litter a year. Possibly the habitat may have much influence upon their behavior. Many of them live in deserts or on their fringes.

The Heteromyidae are nearly all polyestrous for most of the year, but reproduction appears to be in abeyance in late summer and fall.

The Cricetidae and Muridae are alike in being mainly polyestrous all the year, especially under laboratory conditions. In the wild, however, litters tend to be few in July and August and again in the winter. At the latter time the short duration of light appears to be a more injurious factor than the lowered temperature. In species such as these, with an intense rate of metabolism, food supply is probably a major factor in reproduction. A post-parturition heat is the general rule in both families but does not occur in all species, even within a genus. This is especially true in *Peromyscus*. When pregnancy occurs at this time and the females are lactating, delayed implantation and prolongation of gestation is the rule, especially amongst the smaller species. If the female does not become pregnant, lactation anestrum

is the rule. Ovulation is spontaneous, and the corpus luteum of the cycle is nonfunctional, though it is not clear whether this is so in the Gerbillinae. Pseudopregnancy has been recorded in both families, but very few species have been investigated to ascertain whether it is general.

The Caviidae and related families have a longer cycle than the Cricetidae and Muridae. Probably in all of them the corpus luteum of the cycle is functional, as it is in the guinea pig. All species in which it is known have an exceptionally long gestation period for their size.

ANOMALURIDAE

Anomalurus fraseri Waterhouse

SPRING-TAILED SQUIRREL

This squirrel was found pregnant in the North Cameroons in June and July only. It has one young at a time. The penis is surmounted by a cartilaginous spear, and the vagina of the pregnant female is filled with a hard plug (1).

1. Sanderson, I. T. Trans. Zool. Soc., London, 24: 623–725, 1938–40.

Anomalurus pelii Schlegel and S. Müller

FLYING SQUIRREL

This flying squirrel, which inhabits the Gold Coast, bears 2 litters a year, one of them in September (1).

1. Adams, W. H. Proc. Zool. Soc., London, 243–246, 1894.

SCIURIDAE

Citellus beecheyi Richardson

CALIFORNIAN GROUND SQUIRREL

The Californian ground squirrel is apparently polyestrous since in southern California it breeds at any time of the year. In northern California the breeding season is from February to mid-April. The testes decrease in size in May, and by June they are in the abdomen. They are found to be enlarging again in mid-October and are in the scrotum by mid-November. Probably each female has but one litter a year. The number of embryos varies from 4 to 15, and a very extensive series of counts gave a mean of 8.2 (1).

1. Evans, F. C., and R. Holdenried. J. Mammalogy, 24: 231–260, 1943.

Citellus columbianus Ord

COLUMBIAN GROUND SQUIRREL

This ground squirrel, which inhabits an area in British Columbia, Alberta, Washington, Idaho, and Montana, begins to breed about March 15 to 20 (1). Heat lasts 2 to 3 days if the female is unbred, and it returns in 14 to 15 days, continuing thus into May. Gestation lasts 23 to 24 days, usually the latter (2). The number of young varies from 2 to 7, with 2 to 5 usually, and an average of 3.5 (1).

1. Howell, A. H. North American Fauna, No. 56, 1938.
2. Shaw, W. T. J. Mammalogy, 6: 106–113, 1925.

Citellus tridecemlineatus Mitchill

THIRTEEN-LINED GROUND SQUIRREL

This common ground squirrel inhabits central North America. It is one of the small group of animals known to ovulate only after coitus, but, from

their behavior in the field, others of this genus probably fall into this group. Owing to the difficulty of keeping it in good reproductive health in the laboratory there has been a certain amount of confusion in the record of this species, but the main points of interest are now clearly emerging.

The ovaries begin to hypertrophy about January 1, while the females are hibernating. Upon their emergence, about the third week in April, these organs are fully developed and the females are ready to reproduce. The accessory organs follow the ovaries closely in their development. Older animals emerge in a more advanced state of reproductive activity than do younger ones. No effects upon the female have been observed when light, temperature, or diet have been altered in, or before, hibernation. The state of hibernation is said to be a prerequisite for reproduction in the female, though not in the male (1). Anestrum lasts from July to April (2).

The unbred female experiences persistent heat lasting 2 to 4 weeks; these periods recur irregularly at intervals of 2 to 4 weeks. Ovulation does not occur in the absence of copulation, but with copulation it takes place after an interval of 8 to 12 hours (2). The act of copulation lasts for 10 minutes (3). The litter size is 5 to 13, usually 6 to 10 (4), and the period of gestation 28 days (5). There is no postparturition heat (2). In the wild one litter a year is born.

HISTOLOGY OF THE FEMALE TRACT

During anestrum the ovaries are inactive except that there is a good deal of follicular atresia (5). Some of the corpora lutea from the previous breeding season can be seen, but they are in a state of involution. When the females emerge from hibernation, the ovaries weigh 3 to 4 times their anestrous weight. The diameter of mature follicles at the time of heat is about 0.7 mm. During the breeding season the germinal epithelium produces new ova at all times in the cycle. The follicular cavity develops as a split between the granulosa cells at one side of the follicle. The theca externa and interna cannot be distinguished until the follicle is highly cellular (6).

The vulva enlarges considerably during heat. The vagina is small and is closed during anestrum. It enlarges in January and opens in February, remaining open throughout the breeding season, until May or June. It continues large for some months following parturition (5). During anestrum the vaginal epithelium consists of a few layers of small epithelial cells; in proestrum their number increases. The smear in estrus consists of cornified

cells only, but in metestrum leucocytes and cornified and small cuboidal cells are found (7).

During anestrum the uterine muscle is thin and inactive; there is a great growth in proestrum and during heat (2,5). The cells are low columnar or cubical in anestrum and high columnar in heat (5). Glands are scanty and nonsecreting in anestrum, and their lumens are small or absent; in proestrum new glands appear by invagination of the epithelium (2). During heat they are coiled and are secreting (5). At ovulation and during metestrum the epithelial cells decrease in size, as they are actively secreting, while leucocytes appear in the stroma and make their way between the cells (2).

The oviduct is ciliated, with cells 12 to 18 μ in height during anestrum. At the time of heat they have increased to 25 to 30 μ, but again drop to 17 μ at 18 to 24 hours postovulation, after which there is a slight increase to 21 μ (2).

The pituitary gland undergoes seasonal variations in weight and in cell types. Basophils are larger and more numerous during the breeding season, and the granules are also large and numerous. These cells dedifferentiate to chromophobes during the summer. There are no sex differences in cell population. Gonadectomy increases the proportion of basophils, but this effect is prevented or abolished by the injection of gonadic hormones (1).

The adrenal cortex, mainly the reticular zone, hypertrophies during the breeding season and also at other times when the gonads are stimulated by gonadotrophes (1).

PHYSIOLOGY OF THE FEMALE TRACT

Removal of the ovaries during pregnancy results in resorption of embryos or in abortion. Injection of corpus luteum extracts prevents resorption (8). Removal of the uterus during the cycle has no effect upon the ovaries (9). Gonadectomy during anestrum results in a slightly greater degree of atrophy of the accessory organs, so they must secrete a little hormone during this time. The ovaries respond to the injection of anterior pituitary extracts at any time of the year, and estrogens are effective upon the accessory organs of the ovariectomized female at all times (1).

The anterior pituitary is high in gonadotrophes during the breeding season, but they cannot be detected during anestrum. However, gonadectomy increases the potency whenever it is performed (1).

Injection of 100 R.U. of estrogen twice a week for 12 weeks and then three

times a week for 4 weeks induced metaplastic changes in the uterine cornua and glands and in the urethra (10).

THE MALE

The males emerge from hibernation about 2 weeks before the females; the testes at this time are large and scrotal and already contain spermatozoa. By July 1 they have declined in size and have returned to the scrotum. Spermatozoa are no longer present, and the accessory organs have regressed (1). In the laboratory spermatozoa can be found in the adult testis by December; in younger animals they appear in January or February. If breeding males are kept at 4° C. through the spring and summer, they do not undergo sexual retrogression (11).

The pituitary of the male is high in gonadotrophic hormones during the breeding season, when spermatozoa are in the testis, and is extremely low during anestrum. Bilateral castration and low temperatures prevent the fall in potency. In prepuberal males the level is low until a few weeks before spermatozoa appear (11).

Large doses of male urine, P.U., or P.M.S. injected into hypophysectomized males all cause testis enlargement and spermatogenesis. The dose of P.M.S. was 20 to 40 R.U. daily, of Antuitrin S (P.U.) it was 25 to 100 R.U. daily. The shortest time required to produce spermatozoa was 19 days, the optimum length of treatment 30 days (12).

In the normal anestrous male pituitary implants cause descent of the testes in the anestrous period (13), but daily injections of 5 R.U. of Antuitrin S (P.U.) for 12 to 16 days caused enlargement of the testes, spermatogenesis, and development of the accessory organs (14). Spermatogenesis in the ground squirrel is more readily induced by gonadotrophes than it is in any other animal known. Gonadotrophes in doses as low as 2.5 R.U. daily caused some stimulation, even early in anestrum. Bull testis extract at the rate of 6 to 12.5 B.U. daily and male urine at the rate of 6 to 15 B.U. had similar effects, inducing spermatogenesis, but not until late November. The amount of androsterone needed was 1.5 mg. daily (15).

A gonad-stimulating substance is present in the blood serum of the male during the breeding season (16).

The injection of estrogens inhibits the growth of the testes; in castrates it causes growth of connective tissue and muscle in the accessory organs and cornification of the glandular tissue (16).

The anatomy of the male accessories has been studied in detail. The seminal vesicles are large and open separately into the prostatic urethra. The bulbar gland is enormous. The urethra is very broad and muscular with about 13 valvelike folds. The glans penis is broad with a flattened end. It bears hooks which are directed backwards from the os penis and which perforate the epithelium of the glans (17).

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15. Wells, L. J., and C. R. Moore. Anat. Rec., 66: 181–200, 1936.
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Cynomys leucurus Merriam

PRAIRIE DOG

This prairie dog of the west-central United States is sexually active at the age of 1 year (1). The mating season is from the end of March into April and must be of short duration since the reduction of testis size is very abrupt in April (2). The uteri have two cervices, and after copulation a huge plug forms in them. There is a closure membrane across the vagina in the nonbreeding season (1). The ovum is 90 μ in diameter (3). The gestation period is 28 to 32 days. The litter size varies from 2 to 10, with a mode at 5 to 6, and mean of $5.5 \pm .1$ (1).

1. Stockard, A. H. Papers of Mich. Acad. Sci., Arts, and Letters, 11: 471–479, 1929.
2. Stockard, A. H. J. Mammalogy, 10: 209–212, 1929.
3. Stockard, A. H. Papers of Mich. Acad. Sci., Arts, and Letters, 22: 671–689, 1936.

Glaucomys volans L.

FLYING SQUIRREL

The North American flying squirrel may breed several times a year, probably usually twice. Mating begins in late February and early March, and it has been observed again in July. The testes descend in late January or early February and are retracted in September. The vagina is closed by a membrane which opens during heat. At this time the vulva swells to five times its former size, and the vaginal epithelium cornifies. In an isolated female the vulva remained in a swollen state for 5 days, subsided for 11 days, and then again became swollen. She did not have another heat until the following year. The period of gestation is 40 days, and the litter size 1 to 4, usually 3 to 4, with a mean of 3.1 (1). A compilation of available litter sizes gave a mean of $2.93 \pm .13$.

The male has a genital system which is large in proportion to the body size. The testes are very large and thick, the seminal vesicles and bulbar glands are large, the prostate and Cowper's glands are very large. The penis has a very long, saw-edged baculum 20 mm. in length (2).

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2. Mossman, H. W., L. W. Lawlah, and J. A. Bradley. Am. J. Anat., 51: 89–155, 1932.

Marmota marmota L.

MARMOT

This European marmot breeds about April. From the end of August onwards the testes are small, and the interstitial cells are laden with yellow-brown pigment. In March there is great testis growth, and spermatozoa may be found at the end of the month. The interstitial tissue grows and

loses its pigment. At the end of April spermatogenesis ceases, but the interstitial tissue does not regress till July, when the testes return to the abdomen (1). The gestation period is given as 35 to 42 days (2).

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2. Kenneth, J. H. Gestation Periods. Edinburgh, 1943.

Marmota monax L.

WOODCHUCK, GROUND HOG

The breeding season of this North American marmot is in March and April. It breeds at 1 year of age. The gestation period is 28 days, and the average litter size is 4.07. There is practically no difference in the number of embryos in each horn of the uterus (1).

The interstitial cells of the ovary gradually enlarge during winter; after hibernation they become 3 to 4 times their original diameter. The maximal increase, due mainly to an accumulation of lipid and secretion granules, is found in females which do not become pregnant until late in the breeding season. The cells retrogress when corpora lutea are present. The latter persist for many weeks after parturition, but all have retrogressed by September. In the fall a number of fairly large graafian follicles may be observed (2).

The testes show growth similar to that of the ovaries, but the changes are more sudden. The interstitial cells are at a minimum during late summer and fall, beginning to decrease in July when the testes retire to the abdomen. Free spermatozoa are present by the end of March, and regression sets in at the end of April. There is a new cycle of activity beginning in May, and the testes remain active for another two months. During the quiescent period the interstitial cells are laden with pigment, which disappears during the breeding season when these cells are at a maximum. The changes are similar to those observed in the European *M. marmota* (3).

The seminal vesicles have relatively coarse tubules, the bulbar gland is small, the penis is short, and the testes are abdominal most of the year (4).

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Sciurus carolinensis Gmelin

GRAY SQUIRREL

This gray squirrel of eastern North America has been introduced to Great Britain, where it is now common in the wild state. Most of the work upon its reproduction has been done in that country and that work is reviewed first.

This squirrel experiences anestrum from September to January. The young seem not to breed during the year in which they are born although adult weight is reached in their first fall. They may have a second litter in the year; limited evidence suggests two breeding peaks, in March and June, and this may be due to two pregnancies. If practically all the females become pregnant early in the season, they would be unable to reproduce again until the first brood is weaned as there is no postparturient heat (1).

The ovary does not regress much during anestrum. The number of ripe follicles at heat was found to average 4.7 in a limited series, the number of corpora lutea of pregnancy, 3.6, and the number of embryos, 3.6. The size of the mature follicle is about 1.1 mm., and that of the corpus luteum of pregnancy 1.0 to 1.3 mm. The latter begins to regress at mid-pregnancy. The ovum size is 95 μ. There is very little interstitial tissue in the ovary, but a large amount of fibrous tissue is present (1).

The vaginal orifice is closed before puberty and during anestrum. The vulva swells during heat and forms a papilla 0.5 cm. wide and 1 cm. long, which probably remains for 2 weeks. During heat the vaginal epithelium hypertrophies, cornifies, and sloughs off, followed by an invasion of leucocytes. A vaginal plug is formed at copulation (1).

The uterus is bicornuate and the outer coats of the cornua anastamose for 0.5 cm. before the fusion of the circular muscle, which is unusually thick. During anestrum the stroma is dense and poorly vascularized, the glands are few and small, the epithelial cells are 7 to 12 μ high, and hyalinized blood vessels are found in the serosa. During heat all the tissues grow, the stroma becomes edematous, and the cell nuclei enlarge. Vascularity increases, the epthelial cells increase to 15 to 20 μ in height, and the lumen fills with fluid. In metestrum the endometrium becomes folded, the epithelial cells increase further to 25 to 30 μ, and the glands proliferate and become coiled though they are not secreting; they open into depressions between the epithelial

folds. Changes in the cervix are similar to those in the uterine horns (1).

The oviduct is 50 to 60 mm. long and is much coiled. Some cilia are found during anestrum; during heat they increase in numbers, the epithelium is higher, and the interciliary cells are actively secreting (1).

In Texas there are two principal breeding seasons, in winter and summer. The winter season begins in December and the summer one in late May or early June. The average litter size is 2.7, range 1 to 4, usually 2 to 3. The period of gestation is about 44 days (2). In Kentucky the times of breeding are similar, with larger litters often in the winter season (3).

The reduction in testis size is not great in the anestrous period, and the testes are readily retractable at any time. The seminal vesicles are relatively small, slightly branched, and much coiled; they open into the urethra. The prostate and bulbo-urethral glands are large (4).

In Great Britain there is no true anestrous period in the male. The seminal vesicles are bent back upon the prostate. The bulbo-urethral glands are spirally wound. The penis is sharply reflexed at the distal end. There is no fat accumulation in the interstitial cells of the testis (5).

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Sciurus (*Tamiasciurus*) *hudsonicus* Erxleben

AMERICAN RED SQUIRREL

The red squirrel ranges from the Rocky Mountains of North America eastwards. In Manitoba it mates in late March and early April and has one litter annually (1). In the East it has a second litter in August or September. The litter size is 3 to 6, and gestation lasts about 40 days (2). Embryo counts gave an average of 4.2 (3).

The female has an unusually long, coiled vagina during heat. In the male Cowper's glands are minute and open to the urethra in the bulb without a penile duct. There is no bulbo-urethral gland. The seminal vesicles are excessively large. The penis is long and filiform without a baculum. The

urethra has a diverticulum in the bulbar region (4). The testes descend in January, but there are no spermatozoa in the epididymis until January 20. They decrease in size in June but may enlarge again in July. Spermatozoa are still present in September and October (3).

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Sciurus niger L.

FOX SQUIRREL

The fox squirrel in Michigan has a breeding season which begins in late December and early January. After a decline there is some breeding in March to May. It increases in June and again falls off in July. Two litters a year seem to be the rule, and young born in the spring usually reproduce for the first time in late winter, when they are about 11 months of age. Those which are born in summer do not breed until the following spring or summer (1).

The litter size, a combination of embryo counts, number of young in nests, and number of placental sites, is $3.02 \pm .07$; mode, 3; and range, 1 to 6. The gestation period is believed to be about 45 days (1).

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Sciurus vulgaris L.

EUROPEAN RED SQUIRREL

In Russia the breeding seasons of the red squirrel are from January to March and from mid-May to June, but in the South four ovulations a year

may occur, extending the breeding season through March and April and occasionally into August and September. The inference may be drawn that this species is polyestrous under favorable conditions (1). In England pregnant females have been found in every month from December to July, but in August most of the females taken indicated by the state of the reproductive tract that anestrum was approaching (2). Puberty is reached at 11 to 12 months of age, and the gestation period is 32 to 40 days (1).

Sexually active males are found in England from November to July inclusive, possibly longer (2).

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Tamias striatus L.

EASTERN CHIPMUNK

The chipmunk is probably polyestrous; it breeds from March onward, and young born late in the previous season may mate and produce young in July and August. The number of young is 3 to 5, and the gestation period, 31 days (1). In some districts the litter size may be higher, as an average of 5.02 has been reported (2). Puberty is reached at the age of 2½ to 3 months (3).

The oviduct enters the uterus at an angle of 120 degrees. The tubo-uterine junction has a thick mucous membrane, especially on the uterine side, which is extended as a flap. Muscular development in this region is slight (4).

The males are producing spermatozoa by February (2), and the testes are abdominal in the nonbreeding season. The seminal vesicles are relatively large, the prostate small and more egg-shaped than in the true squirrels. It has a prominent reservoir portion. The bulbo-urethral glands are small, and the bulbar glands are without an intermediate portion (5).

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Other SCIURIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Citellus beldingi Merriam	One litter a year, born Apr. 10–20 (N.A.F. 56). Born June in *oregonus* subsp. (N.A.F. 55)	4–12, av. 8		Oregon, Nevada, California
C. citellus L. Suslik			25 days	
C. franklinii Sabine	One litter a year, mates mid-May (Seton)	4–10		Great Plains of N. America
C. harrisii Audubon and Bachman Antelope Squirrel	Mid-Jan.–Mar. (N.A.F. 55)	6		Arizona and northern Mexico
C. idahoensis Merriam	March (N.A.F. 56)	8–10		Snake River Valley, Idaho
C. lateralis Say Mantled Ground Squirrel	One litter a year, May–July (N.A.F. 53, 56)	2–8		Western N. America
C. leucurus Merriam Antelope Squirrel	Early Apr., second litter July (N.A.F. 53)	6–8		California and neighboring states
C. mohavensis Merriam Mohave Ground Squirrel	Early to mid-March (N.A.F. 56)	6		Mohave region of California. 1 record
C. parryii Richardson Parry's Ground Squirrel	Born mid-May to early July (N.A.F. 56)	5–7		Arctic N. America

Other SCIURIDAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
C. richardsonii Sabine Yellow Ground Squirrel	One litter a year, mate mid-Apr. (Seton)	2–11, varies from year to year, mode 6	28–32 days	S.W. Canada and northwestern U.S.
C. spilosoma Bennett Spotted Ground Squirrel	Two litters a year (Davis and Robertson)	5–8, mode 6–7		Western N. America
C. tereticaudus Baird Ring-tailed Ground Squirrel	May have 2 litters a year, born March–Apr. (N.A.F. 56)	5–12		Extreme southwestern U.S. and N.W. Mexico
C. townsendii Bachman	One litter a year, breeds March–Apr. (Davis)	4–16, av. 8.6, mode 8–10, mean 9.5 ± .1		Washington, Idaho, Nevada, W. Utah
C. variegatus Erxleben Mexican Rock Squirrel	May–June, Aug.–Sept., probably 2 litters a year (N.A.F. 53)	5–7		Southwestern U.S. and Mexico
C. washingtoni Howell	Mate early Feb. (Scheffer)	5–11, av. 8.0		Washington, W. Idaho
Cynomys gunnisoni Baird Prairie Dog	Apr.–May (Mearns)	3–6, av. 4.8		Southwestern U.S.
C. ludovicianus Ord Plains Prairie Dog	Born May–July, begins to breed Feb. in Kansas (Wade)	2–10, mode 5, mean 5.0 ± .16		Cent. and southwestern N. America
Eutamias amoenus Allen Chipmunk	Born Apr.–July (N.A.F. 55)	4–5		Western N. America

Other SCIURIDAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
E. cinericollis Allen Gray-collared Chipmunk	Probably 1 litter a year, born June–July (N.A.F. 53; Mearns)	3–5		Southwestern U.S.
E. dorsalis Baird Cliff Chipmunk	Two litters a year (N.A.F. 53), born July (Mearns)	2–8		Utah and New Mexico
E. merriami Allen	Born May to early June (Mearns)			S. California and N. Mexico
E. minimus Bachman Little Chipmunk	Born early May to June (N.A.F. 55)	4–7		West-central U.S.
E. quadrimaculatus Gray	Born May (Ross)		31 days	California
E. quadrivattus Say Long-tailed Chipmunk	Mate Apr., 1 litter a year, or 2 in favored districts (N.A.F. 53)	2–6		South-central U.S.
Bachman *E. townsendii*	Mate March–Apr., born May–June (N.A.F. 55)	4–6		Western U.S.
Geosciurus inauris Zimmermann South African Ground Squirrel	Breeds twice a year	2–6, usually 4		S. Africa. Puberty at 6 months (Powell)
Glaucomys sabrinus Shaw Flying Squirrel	Probably 2 litters a year (Hamilton); 1 in north (Cowan). Mate late winter (Hamilton)	2–6, usually 4		Canada and northern U.S.

Other SCIURIDAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Marmota caligata Eschscholtz Woodchuck		5		Northwestern N. America. 1 record
M. flaviventris Audubon and Bachman	Mate March, born May (N.A.F. 55)	8		Western N. America. 1 record
Microsciurus alfari Allen Pygmy Squirrel	Apr.–June (Enders)			Cent. America
Paraxerus cepapi A. Smith Gray-footed Bush Squirrel		2–4		Cent. and S. Africa
P. ochraceus Huet Bush Squirrel	Nov.–Dec. (Abbott)	2		Kenya and Tanganyika
Pteromys magnificus Hodgson Hodgson's Flying Squirrel	Breeds in rains (Blanford)	1		India
Sciurus aberti Woodhouse Abert's Squirrel	More than 1 litter a year (N.A.F. 53), May–Aug. (Mearns)	3–4		Southwestern N. America
S. apache Allen		3		Mexico. 1 record
S. caniceps Gray Golden-backed Squirrel	Spring (Blanford)	1		India
S. deppei Peters		3		Mexico and Cent. America. 1 record

Other SCIURIDAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
S. douglasii Bachman Orange-bellied Chickaree	Season irregular (N.A.F. 55)	4–7, usually 4		Western N. America
S. fremonti Audubon and Bachman Chickaree	Born spring to early summer; 1 litter a year (N.A.F. 53)	1–4		Rocky Mountains
S. gerrardi Gray	Breed May (Enders)	1–3, usually 2		Panama
S. griseus Ord	Born Jan.–Feb. in Oregon; May–June, Mexican border (N.A.F. 55; Mearns)	4		Western N. America
S. hoffmanni Peters		3		Cent. America. 1 record (Enders)
S. (*Funambulus*) *palmarum* L. Palm Squirrel		2–4		India

MUSCARDINIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Claviglis kelleni Reuvens Tree Dormouse		2, 5		S.W. Africa. 2 records

MUSCARDINIDAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
C. murinus Desmarest Cape Dormouse	Short breeding season at mid-summer, Dec.–Jan. (Fitz-simons)	4–5		Cent. and S. Africa
C. nanus De Winton		4		Rhodesia. 1 record
Eliomys quercinus L. Dormouse	Polyestrous, cycle about 10 days (Lataste)		22 days	Europe. Copulation plug formed
Muscardinus avallanarius L. Common Dormouse	Polyestrous (?), May–Oct. (Barrett-Hamilton)	2–7	21 days	N. Europe

GEOMYIDAE

Geomys bursarius Shaw

POCKET GOPHER

This pocket gopher of North America has one litter a year in the wild state, and the young are born in March and April. The litter size varies from 1 to 6, mean 3.8, and mode 4 (1).

The oviduct is somewhat peculiar; the isthmus is very sharply and regularly coiled, forming a conical mass with its apex at the junction with the ampulla. It is very muscular. The ovaries are not encapsulated. The uterine horns are relatively short and thick, and are fused externally for 1.5 cm. above the two cervices (2). The theca interna is very thick, and the type of cells suggests that it is an endocrine gland. It reaches its greatest development during proestrum and heat. After ovulation it rapidly degenerates and takes no

part in the formation of the corpus luteum, though it does form interstitial cells. It seems to be the only source of the latter (3).

In castrated and normal males the injection of ovarian extracts (relaxin) causes the symphysis pubis to be reabsorbed. Testis grafts into ovariectomized females prevent resorption of the calcium in the pubic bones (4).

1. Scheffer, T. H. Kansas Agric. Exp. Sta., Bul. 152, 1908.
2. Mossman, H. W., and F. L. Hisaw. Am. J. Anat., 66: 367–391, 1940.
3. Mossman, H. W. Am. J. Anat., 61: 289–319, 1937.
4. Hisaw, F. L. J. Exp. Zool., 42: 411–441, 1925.

Other GEOMYIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Cratogeomys castanops Baird Chestnut-faced Pocket Gopher		3		South-central N. America. 1 record
Geomys breviceps Baird	One litter a year. March–May (English)	1–3, av. 2.36		South-central N. America
G. floridanus Audubon and Bachman Southern Pocket Gopher	One litter a year (Hamilton)	3–4		
Thomomys bottae Eydoux and Gervais Pocket Gopher	Polyestrous, early March onwards (Scheffer)	Av. 5.85		California
T. bulbivorus Richardson	One litter a year. March–July (Scheffer, Wight)	5–9, usually 5, av. 4.2		Oregon
T. douglasii Richardson	Feb.–March, testes regressing in May (Scheffer)	Av. 5.0		Washington, Oregon

Other GEOMYIDAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
T. fossor Allen	Born May–June, 1 litter a year (N.A.F. 53)	4		Central N. America
T. fulvus Woodhouse	One litter a year (N.A.F. 53); most of year (Alcomb)	1–7, av. 3.8		Central and southwestern N. America
T. fuscus Merriam	Polyestrous, spring and summer (N.A.F. 55)	Av. 6.3		Western N. America
T. monticola Allen	Polyestrous, spring and summer (N.A.F. 55)			
T. ocius Merriam		6–7		Wyoming, Colorado, Utah
T. perpallidus Merriam	Polyestrous, all year (Scheffer)	Av. 3.9		Southwestern U.S.
T. quadratus Merriam	March on, at least 2 litters a year in quick succession (Wight)	1–7, embryos usually 6–7; young found usually 2–3	40 days	Northwestern U.S.
T. talpoides Richardson	One litter a year, born June (Criddle)	1–5, av. 3.0 $\pm .24$		Central N. America
T. townsendii Bachman	Polyestrous, spring–summer (Horn)	3–10, 6–7 usual, av. 6.8 $\pm .3$		Western N. America
T. umbrinus Richardson		2–3		Mexico

HETEROMYIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	HABITAT, ETC.
Dipodomys hermannii Le Conte Kangaroo Rat	Feb.–Aug. (Jappe)	2–4, mode 4	California
D. ingens Merriam Giant Kangaroo Rat	Jan.–May (Grinell)	5–6	California
D. merriami Mearns	Polyestrous (Alcorn)	2–4, av. 3.1	Southwestern N. America
D. microps Merriam	Spring and fall (Duke)	2–4	Western U.S.
D. ordii Woodhouse	Probably polyestrous, young spring–fall (Warren, Alcorn)	1–5, av. 3.6	Central and Western N. America
D. spectabilis Merriam	Jan.–Aug., mostly April (Duke)	1–3, mode 2, av. 1.81 ± .04	Southwestern N. America. A copulation plug is formed (Vorhies and Taylor)
Heteromys desmarestianus Gray		3–5	Mexico and Cent. America (Enders)
H. gaumeri Allen and Chapman		2	Mexico. 1 record
Microdipodomys megacephalus Merriam Pygmy Kangaroo Rat	Probably polyestrous, most born May–June (Hall and Linsdale)	1–6, av. 4.0	Nevada, Oregon
Perognathus fasciatus Wied Pocket Mouse	Spring–summer, probably 1 litter a year (N.A.F. 49)	4–6	Central U.S.

HETEROMYIDAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	HABITAT, ETC.
P. flavescens Merriam		4	Central U.S.
P. flavus Baird	Probably poly-estrous (N.A.F 53)	2–6	Central and south-western N. America
P. formosus Merriam		4	Utah. 1 record
P. hispidus Baird		5	Central and south-western N. America. 1 record
P. lordi Gray	Probably poly-estrous, early May–Aug. (Scheffer)	2–8, usually 4–5; mean 5.1 ± .1	Western N. America
P. nevadensis Merriam		3–4	Nevada, Oregon, and Utah. 2 records
P. parvus Peale	Summer (N.A.F. 55)	3–6	Western N. America

CASTORIDAE

Castor canadensis Kuhl

BEAVER

There is little accurate knowledge of the breeding of the beaver, mainly because of its aquatic habitat. Mating usually occurs in January and February, and there is one litter a year, born in April and May. Puberty is at 2 years of age (1). The number of young born is usually 3 to 4, but it varies from 1 to 6. Embryo counts from various sources have given 1 to 8, average 3.68 ± .12, mode 4. Gestation has been variously stated to be from 42 to 128

days, with most authorities giving "about 3 months." A pair seen copulating gave a probable observed gestation period of 128 days (2). The sex ratio of embryos is approximately equal, 24 males to 22 females (3).

1. Seton, E. T. Life Histories of North American Animals. New York, 1909.
2. Bradt, G. W. J. Mammalogy, 20: 486–489, 1939.
3. Bradt, G. W. J. Mammalogy, 19: 139–162, 1938.

CRICETIDAE

CRICETINAE

Cricetulus griseus Milne-Edwards

CHINESE HAMSTER

The estrous cycle of the Chinese hamster lasts for 4 days, with an average of $4.3 \pm .08$ days, and there is no restricted breeding season. The vaginal smear resembles that of the rat and mouse, but the stages are more definite. Epithelial cells are present for 2 to 3 days, nucleated epithelial cells only for less than 1 day, and cornified cells for 1½ to 2 days, with ovulation toward the end of this stage. The proestrous stage lasts ½ day, estrus 1½ days, and diestrum or metestrum 2½ days. Ovulation is spontaneous, and the corpus luteum suffers a precipitous decline after 2 days of diestrum, in contrast to the condition in the rat and mouse. The mature follicle measures 0.45 mm. in diameter (1). It seems not to have been determined whether the corpora lutea would persist and pseudopregnancy result if sterile copulation were permitted. This would be interesting to know in view of the decline of the corpus luteum, and it would probably occur as it does in the similar type of cycle recorded for *Cricetus auratus*.

The ovaries resemble those of the rat and mouse. They are bean shaped and are completely enclosed within a fibrous capsule. The oviduct is long and much coiled. The uterus is bicornuate, and the horns fuse just above the cervix. The clitoris is large and it is perforated by the urethra (1).

During diestrum the uterine mucosa has a low columnar epithelium, leucocytes are present in the stroma, and the glands are inactive. In proestrum the epithelium is the same as in diestrum, but no leucocytes can be found

and the glands are secreting. In estrus the epithelial cells are tall and apparently pseudostratified. The glands are emptying, and, toward the end of this stage, leucocytes make their way into the stroma (1).

In some specimens sent from China a series of large glandular bodies about 1.5 to 2.0 mm. in diameter were present in the uterus on the mesometrial side. From 8 to 10 were found in each cornu, and as they closely resemble corpora lutea it is believed that they may have a glandular function (1).

1. Parkes, A. S. Proc. Roy. Soc., 108B: 138–147, 1931.

Cricetus auratus Waterhouse

GOLDEN HAMSTER

The Syrian hamster first comes in heat at 7 to 8 weeks of age (1) or at a weight of about 60 g. The females are polyestrous and come in heat at any time of the year, though pregnancies are infrequent from October to March. The failure in reproduction seems to be due to the male rather than to the female, and better reproduction can be obtained during the winter by exposing the animals to an increased amount of light. The estrous cycle lasts for 4 days with little variation, but a mated female which does not become pregnant experiences pseudopregnancy which lasts 7 to 13 days, usually 9 to 10 days, mean 9.6 ± .2 days. Mating is nocturnal and usually occurs after 10 P.M. (1), or 8 P.M. (2), but it is also frequent before 9 A.M. (3). Ovulation is usually a few hours later. The bicornuate copulation plug is extruded rather soon, as a rule. There is no postparturient heat or ovulation, and, if the female is lactating, heat does not occur during this time. The litter size varies from 1 to 12 (4) with 6 to 7 as the modal size (1). Few females have more than 3 to 4 litters; subsequently they usually abort or do not become pregnant although they may come in heat regularly. The period of gestation is 16 days (4), though it may last as long as 19 days (5). The sex ratio is 54.7 per cent males (1).

The ovaries are small and completely encapsulated. The ovum is 60 to 63 μ in diameter and the ripe follicle, 690 to 780 μ. At heat the theca interna becomes very congested, and 10 to 13 follicles usually rupture at this time. The corpora lutea develop rapidly, and those of the normal cycle decline precipi-

tously after about 3 days, in contrast to the condition in rats and mice. In this type of corpus luteum, which appears to be nonfunctional, the lutein cells do not increase much in size. In the pseudopregnant corpus luteum the lutein cells are larger and vascularization is much greater. Regression sets in at 7 days. There are differences in the sizes of the various types of corpora lutea:

Size of corpus luteum of cycle	700 μ
Size of corpus luteum of pseudopregnancy	820–860 μ
Size of corpus luteum of pregnancy	900–1,000 μ

Regression of the corpus luteum of pregnancy is rapid after parturition (4).

The vagina may be divided into two parts, that comprising 1 cm. from the vulva, and the upper portion. The lower portion is continually growing cornified cells, which fill two lateral ventral pouches. If the region is squeezed, these cells may be extruded as two leaflike processes at any time of the cycle. Accordingly, the vaginal smear is not a good indication of the reproductive state. The epithelium of the upper vagina contains many mucous cells which are shed in large numbers after heat. In this region there are remarkable epithelial growths during heat. These consist of epithelial villi with 3 to 8 layers of cornified cells covered with irregular foliations of epithelial cells with oval nuclei. After ovulation these masses are shed and polymorphs invade the region. After mating the desquamated area regenerates and becomes covered with columnar cells which mucify (4).

Others have found that the smear carefully taken from the upper vagina is a reliable indication of heat. The proestrous smear consists of a few small cornified cells with a very few leucocytes. This changes to a few small cornified cells during heat, and it is followed by an invasion of leucocytes together with nucleated epithelial cells. The smear between heats is abundant, and it consists mostly of nucleated epithelial cells and leucocytes with a few large cornified cells (2). The evening before heat and on the day of heat the smear is sticky, changing to waxy. (3).

The oviducts and uterus resemble those of the rat and mouse in their reactions (4).

Ovariectomy between 11 and 13 days of pregnancy results in abortion. Progesterone alone fails to continue the gestation, but if estrogen is given simultaneously it goes on to term. If the uterus is removed from the eighth to the thirteenth day of pregnancy, estrous cycles are resumed, but if the embryos only are removed and the placentae retained, cycles are inhibited (6).

If estrogens are injected into the spayed female, completely cornified vaginal smears are produced, a condition never found in the normal female (but see above for conditions in the upper vagina). Progesterone has very little effect upon uterine histology (7).

1. Bruce, H. M., and E. Hindle. Proc. Zool. Soc., London, 361–366, 1934.
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3. Ward, M. Personal communication.
4. Deansley, R. Proc. Zool. Soc., London, 108A: 31–37, 1938.
5. Ben Menahem, H. Arch. Inst. Pasteur, Algiers, 12: 403–407, 1934.
6. Klein, M. Proc. Roy. Soc., London, 125B: 348–364, 1938.
7. Peczenik, O. J. Endocrinol., 3: 153–163, 1943–44.

Neotoma fuscipes Baird

WOOD RAT

This wood rat has a wide range in the mountains and valleys of the western United States, and the differences in climate which it encounters may explain some of the discrepancies reported in its reproduction.

The females are probably polyestrous (1). The testes enlarge in December (2), or from January to March, but there is a little breeding in July and August (3). No vaginal plug is produced after mating, and in two cases the duration of gestation was 33 days (2). The number of embryos, compiled from several sources, is usually 2 to 3, with a range of 2 to 4 and a mean of $2.68 \pm .08$.

1. Warren, E. R. J. Mammalogy, 7: 97–101, 1926.
2. Wood, F. D. J. Mammalogy, 16: 105–109, 1925.
3. Vestal, E. H. J. Mammalogy, 19: 1–36, 1938.

Oryzomys palustris Harlan

RICE RAT

The rice rat of the eastern United States is polyestrous and breeds from February to November. The female reaches puberty when 50 days old. The

litter varies from 1 to 5 with an average of 3.0. The gestation period is 25 days, and the female mates immediately after parturition. Young females have smaller litters than older ones (1).

1. Svihla, A. J. Mammalogy, 12: 238–242, 1931.

Peromyscus boylii Baird

WHITE-FOOTED MOUSE

This white-footed mouse which lives in western North America is polyestrous (1). In low country it breeds all the year, but high on the coast range the young are not born until May (2). The age at first heat is 50.9 ± 1.9 days (3). The litter size is 2 to 4, usually 3, and the mean is $3.0 \pm .13$.

1. Bailey, V. North American Fauna, No. 53, 1931.
2. Mearns, E. A. U.S. National Museum, Bul. 56, 1907.
3. Clark, F. H. J. Mammalogy, 19: 230–234, 1938.

Peromyscus californicus Gamble

This mouse is polyestrous and has no heat immediately after parturition, thus differing from most other species of the genus. The mean litter size is $1.87 \pm .09$, with a range of 1 to 3. The mean gestation period is 23.6 with a range of 21 to 25 days (1).

1. Svihla, A. Univ. of Michigan, Museum of Zool., Misc. Publ. No. 24, 1932.

Peromyscus eremicus Baird

DESERT PEROMYSCUS

This mouse is polyestrous and experiences no heat immediately after parturition. One gestation has been observed and it lasted 21 days. The mean

litter size is $2.6 \pm .24$ with a range from 2 to 4 (1). The mean age at first heat is 39.2 ± 1.5 days (2). It breeds all the year except in the mountains (3). Compilation of data on embryo numbers gave a mean of $3.7 \pm .2$, with a range from 1 to 4.

1. Svihla, A. Univ. of Michigan, Museum of Zool., Misc. Publ. No. 24, 1932.
2. Clark, F. H. J. Mammalogy, 19: 230–234, 1938.
3. Mearns, E. A. U.S. National Museum, Bul. 56, 1907.

Peromyscus leucopus Rafinesque

WOOD MOUSE

This widespread North American wood mouse is polyestrous and breeds from early April to the beginning of October in the northern part of its range (1). In the south it breeds at all times (2) but reproduction tends to fall off in July and August (3). Puberty in the female is reached at 46.22 ± 3.18 days (4). The estrous cycle lasts 4 to 5 days, and the vaginal smears are typical, like those of the rat and mouse (5). The litter size is $5.04 \pm .08$, with a range from 3 to 7 in Ontario (1), and $4.09 \pm .08$ in Michigan (6). There appear to be considerable differences, but as younger mice have smaller litters the differences may be due to the age of the animals at the time of observation. Also, the first figures refer to embryos and the second to young born. Four appears to be the modal number of embryos in the wild state.

There is a heat immediately after parturition, and the duration of gestation in the nonlactating female averages 23.2 days. In the lactating female gestation may be prolonged by as many as 14 days (6).

This species has been the subject of research on the influence of light upon the periodicity of breeding. In Michigan most litters are born in May and June, with few in July, and reproduction is more frequent again from late August to October. None are born from December to February. With 1 foot-candle of light to prolong the length of day to 18 hours during the short-day season the mice breed at that time as well as they do in the usual breeding season. Lowered temperature (4° to 6° C.) has no adverse effect if the light is maintained. Intense light is not an advantage. If the mice are blinded,

fertility is not affected, but they do not experience cyclical reproduction. Continued darkness lowers reproduction, and it becomes noncyclical in type (7).

1. Coventry, A. P. J. Mammalogy, 18: 489–496, 1937.
2. Mearns, E. A. U.S. National Museum, Bul. 56, 1907.
3. Burt, W. H. Univ. of Michigan, Misc. Publ. No. 45, 1940.
4. Clark, F. H. J. Mammalogy, 19: 230–234, 1938.
5. Osgood, F. L., Jr. Personal communication.
6. Svihla, A. Univ. of Michigan, Museum of Zool., Misc. Publ. No. 24, 1932.
7. Whitaker, W. L. J. Exp. Zool., 83: 33–60, 1940.

Peromyscus maniculatus Wagner

DEER MOUSE

The deer mouse is widespread throughout North America. The female is polyestrous and tends to breed all the year, but reproduction is often less during midsummer (1,2). In Ontario breeding ceases for the winter about the beginning of September (3). The estrous cycle lasts 4 to 5 days, and the changes in the vaginal smears are like those of the rat and mouse (4). The age at first heat is 48.72 ± 1.23 days (5). The average number of embryos has been given as $5.38 \pm .13$ with a range from 2 to 8 (3). A compilation of other figures, which relate to embryo counts in several subspecies, gives $5.00 \pm .09$. The modal number of embryos is 5 and the range 2 to 9. A series of births gave $4.04 \pm .03$ (6).

The female experiences heat immediately after parturition, and the duration of gestation in the nonlactating female is 23.5 days with a range from 22 to 27 days. Lactation increases the length up to 10 days (6).

1. Hamilton, W. J., Jr. The Mammals of Eastern United States. Ithaca, 1943.
2. Blair, W. F. Am. Midland Nat., 24: 273–305, 1940.
3. Coventry, A. P. J. Mammalogy, 18: 489–496, 1937.
4. Osgood, F. L., Jr. Personal communication.
5. Clark, F. H. J. Mammalogy, 19: 230–234, 1938.
6. Svihla, A. Univ. of Michigan, Museum of Zool., Misc. Publ. No. 24, 1932.

Peromyscus truei Schufeldt

This deer mouse of western North America is probably polyestrous and breeds during spring and summer (1). The age at first heat is 50.09 ± 2.44 days (2). A few gestations gave a nonlactating mean of 26.2 ± .3 days, with a range from 25 to 27 days, a little longer than is usual in this genus of mice. A single gestation in a lactating mouse lasted 40 days. The mean litter size at birth was 2.84 ± .14, with a mode of 2, considerably less than the usual number for the genus (3). Embryo counts in the field have varied from 3 to 6 for a limited series.

1. Warren, E. R. The Mammals of Colorado. Stillwater, Okla., 1942.
2. Clark, F. H. J. Mammalogy, 19: 230–234, 1938.
3. Svihla, A. Univ. of Michigan, Museum of Zool., Misc. Publ. No. 24, 1932.

Reithrodontomys megalotis Baird

HARVEST MOUSE

This mouse is widespread in North America. The female is polyestrous and breeds all the year round, but mostly from April to October, with a tendency to reduced breeding at midsummer (1). The duration of gestation is 23 to 24 days; the litter size at birth is 1 to 7, mean 2.6 ± .2. The earliest breeding age is 4 months 8 days (2). Embryo counts have ranged from 1 to 7, with a mean of 4.1 ± .2.

1. Smith, C. F. J. Mammalogy, 17: 274–278, 1936.
2. Svihla, R. D. J. Mammalogy, 12: 363–365, 1931.

Sigmodon hispidus Say and Ord

COTTON RAT

This cotton rat of southern North America is polyestrous in the wild, breeding from early spring to late fall, or longer (1). In the laboratory it

breeds all the year round. The testes descend usually at 20 to 30 days, varying from 10 to 50 or more days, and the vaginal introitus is established at 30 to 40 days, as a rule, with a variation from 10 to 50 or more days. Puberty is reached earlier in the spring than it is in the fall. Spermatozoa are produced at 40 to 50 days of age (2).

The vaginal smear is characteristic of the Muridae and Cricetidae. There is a reduction in the number of leucocytes and an increase in nucleated epithelial cells during proestrum, with cornified cells in estrus, and nucleated epithelial cells followed by leucocytes in metestrum. The lengths of the parts of the cycle are most variable, and the following ranges have been found (2):

Proestrum,	average	14 hours,	12– 21 hours range
Estrus,	average	46 hours,	21–123 hours range
Metestrum,	average	14 hours,	9– 21 hours range
Diestrum,	average	116 hours,	42–156 hours range

Another account gives vaginal heat as lasting on the average 3.4 days, range 1 to 12 days, and a cycle length of 9 days, range from 4 to 20 days. The uterus is distended during heat, and ovulation occurs late in this period. The post-parturition heat lasts 18 to 24 hours, a shorter period than that of the normal cycle, and ovulation occurs 6½ to 12 hours after littering. A vaginal plug is formed at coitus. The eggs take about 60 hours in their passage through the oviduct, and remain for nearly half that time in the last third. The placental sign, erythrocytes in the vagina, is given on the tenth day of pregnancy (3).

The average litter size is 5.6, with a range from 2 to 10, and the sex ratio at birth is 51.7 per cent (3). Other mean litter sizes are 4.75, range 3 to 8 (1), and 7.4, range 5 to 10 (4). Apparently, it is variable in different districts or on different feeds. For the subspecies *chiriquensis* Enders has records of 2 and 3 embryos, lower than the usual number for the species. The duration of gestation is 27 days, and suckling has little effect upon its length (3).

1. Svihla, A. J. Mammalogy, 10: 352–353, 1929.
2. Clark, F. H. Contrib. Lab. Vert. Genet., Univ. of Michigan, 1936.
3. Meyer, B. J., and R. K. Meyer. J. Mammalogy, 25: 107–129, 1944.
4. Rinker, G. C. Trans. Kansas Acad. Sci., 45: 376–378, 1942.

Other CRICETINAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Baiomys taylori Thomas	Polyestrous	2.72 ± .13	20 days	Southwestern U.S. and Mexico. Puberty about 44 days (Blair)
Cricetulus triton De Winton Giant Hamster	March to mid-May (Loukashkin)	4–6, usually 6		Manchuria. Testes enormous, up to ⅕ of body weight
Cricetus cricetus L. Common Hamster	Testes active in March, resting in Sept. (Kayser and Aron)	4–18, usually 6–12	20 days	Cent. Europe to Russia and Asia Minor.
Neotoma albigula Hartley Wood Rat	Polyestrous, Apr.–Sept., or all year (Feldman)	1–3, 2.24 ± .09	<30 days	Western N. America
N. cinerea Ord	Spring to early summer, 1 litter a year in north, probably more in south (Dixon)	1–6, usually 4. 4.0 ± .25		Western N. America
N. desertorum Merriam		5		Western N. America. 1 record
N. floridana Ord Florida Wood Rat	Polyestrous (Dice) all year (Hamilton)	1–4, usually 3–4		Southwestern U.S.
N. lepida Thomas Desert Wood Rat	Feb.–May, polyestrous (Long)	2–5, usually 3		Southwestern U.S.
N. magister Baird	Polyestrous, late Feb.–Sept. (Poole)	1–3, usually 2	30–36 days	Eastern U.S.

Other CRICETINAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
N. mexicana Baird Mexican Wood Rat	Probably polyestrous (N.A.F. 53)	2–4, usually 2–3		Southwestern N. America
N. micropus Baird	Polyestrous, late Apr. on (N.A.F. 53), 1 litter a year, born Feb. in captivity (Feldman)	2–3 $2.27 \pm .08$	33 days	Western N. America
Oecomys endersi Goldman		3		Panama. 1 record
Onychomys leucogaster Wied Grasshopper Mouse	Polyestrous, Apr. to Sept. (Warren)	2–6, usually 4	33 days	Cent. and western N. America. Gestation longer (39–47 days) when lactating. Female puberty 90 days (Svihla)
O. torridus Coues		3–4		Western N. America
Oryzomys alfaroi Allen		7		Cent. America. 1 record
O. couesi Alston		1–6, usually 5		Mexico and Cent. America
O. devius Bangs		3–4		Panama (Enders)
O. fulvescens Saussure Rice Rat		2–5, mean $3.5 \pm .1$, mode 3		Cent. America (Enders)
O. talamancae Allen	Probably polyestrous (Enders)	3–4, usually 4		Cent. America

Other CRICETINAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Ototylomys phyllotis Merriam		1–3, usually 2		Mexico
Peromyscus crinitus Merriam		2–4		Cent. and western N. America
P. gossypinus Le Conte	Polyestrous, all year (Hamilton)			Southeastern U.S.
P. nasutus Allen		3–6, usually 4		West-central U.S.
P. nudipes Allen		2–3		Cent. America (Enders)
P. nuttalli Harlan	Polyestrous, Apr.–Sept. (Brimley)			Eastern and southern U.S.
P. polionotus Wagner				Southeastern U.S. Age at first heat, 29.64 ± 0.47 days (Clark)
P. yucatanicus Allen and Chapman		2		Mexico. 1 record
Reithrodontomys albescens Cary Harvest Mouse		3–5		Central U.S. 3 records
R. creper Bangs		2		Panama. 2 records (Enders)
R. fulvescens Allen		2		Texas and Mexico. 1 record
R. humilis Bachman	May–Nov. (Brimley)	2–5		Eastern and southern U.S.

Other CRICETINAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
R. mexicanus Saussure		2–5		Mexico and Cent. America (Enders)
R. montanus Baird		2–4, $2.9 \pm .15$	21 days	Colorado. Puberty at 2 months (Leraus)
Scotinomys teguina Alston		2		Cent. America (Enders)
Sigmodon minimus Mearns Least Cotton Rat		3, 4		Southwestern N. America. 2 records
Teanopus phenax Merriam Wood Rat		2		Mexico. 1 record
Tylomys watsoni Thomas		3		Cent. America. 1 record (Enders)
Zygodontomys cherriei Allen Cane Rat	Polyestrous (Enders)	2–4		Cent. America

MICROTINAE

Arvicola amphibius L.

WATER VOLE

This vole, which lives in Great Britain, is polyestrous, with a breeding season from the end of March to the end of September, but males are ready to reproduce in February. Animals born early in the year breed during the same season, but cycles in adult females at the beginning of the season may be infertile. There is a postparturient heat and a lactation anestrum. The average number of corpora lutea is 6.4, and of embryos 5.7 (1), or 5.6 (2).

The ripe follicle is 700 μ in diameter. The corpus luteum reaches its maximum size, 1.7 mm., fairly late in pregnancy. Large follicles are found at all stages of pregnancy. The diameter of the ovum is 80 μ. The uterus is distended with fluid during heat (1).

1. Perry, J. S. Proc. Zool. Soc., London, 112A: 118–130, 1942.
2. Barrett-Hamilton, G. E. H. A History of British Mammals. London, 1910.

Clethrionomys (Evotomys) gapperi Vigors

RED-BACKED MOUSE

This vole, which lives in North America, is polyestrous and breeds from late winter to late fall in the wild, but all the year in captivity. The females experience postparturient heat. Copulation is very brief and several matings occur in a few minutes, after which the female does not desire more. Gestation is from 17 to 19 days (1). The litter size is from 3 to 8, with a mean of $5.4 \pm .13$ (2).

1. Svihla, A. Papers of Mich. Acad. Sci., Arts, and Letters, 11: 485–489, 1930.
2. Coventry, A. P. J. Mammalogy, 18: 489–496, 1937.

Clethrionomys (Evotomys) glareolus Schreber

BANK VOLE

This European vole is polyestrous, with a breeding season from mid-April to the beginning of October. Reproduction is at a maximum in June, and the females usually bear 4 to 5 litters a year. At the beginning of the season many of them undergo a varying number of cycles, usually 3, before they become pregnant. Females born early in the season reproduce before its close. The spontaneous ovulation is near the end of heat, as copulation occurs before the follicles rupture. A hard copulation plug is formed. There is a postparturient heat. Implantation is delayed during lactation, and in the nonpregnant female lactation anestrum occurs. A winter anestrum is the rule,

and the vagina is closed throughout this period (1). The number of young born varies from 2 to 8 (2), average 3.8 ± .01 (3).

Cyclical changes in the histology of the reproductive tract are similar to those described for the rat and mouse. The ovaries are surrounded by a closed capsule. The number of corpora lutea averaged 4.4, with an observed maximum of 12, and the embryo count was 4.1, with an observed maximum of 6. The number of ovulations increases to a maximum in June and then falls off. The ripe follicle measures 550 to 800 μ; the ovum, 70 μ; and the corpus luteum, 0.8 to 1.2 mm. The maturation spindle is formed before ovulation, but the first division does not occur until after the follicle has ruptured. The uteri open into the vagina by separate cervices and are distended during heat, at which time, also, intense vaginal cornification occurs (1).

In the male sexual activity begins in March. The mean winter weight of the testes is 40 mg., and the mean summer weight 682 mg. Males born early in the season mature before its end, but those born later mature at the beginning of the next year. Regression of the testes begins in August, and spermatogenesis has ceased by November. The seminal vesicles are comparatively large (4).

1. Brambell, F. W. R. Phil. Trans. Roy. Soc., London, 226B: 71–97, 1936.
2. Didier, R., and P. Rode. Mammalia, 3: 111–121, 1939.
3. Barrett-Hamilton, G. E. H. A History of British Mammals. London, 1910.
4. Rowlands, I. W. Phil. Trans. Roy. Soc., London, 226B: 99–120, 1936.

Microtus agrestis L.

FIELD MOUSE

The European field mouse is polyestrous, and in Great Britain the breeding season is from February and March to September and October. Breeding starts later, and finishes earlier, in the south than it does in the north of the range (1). By shortening the length of exposure to light from 15 hours to 9 hours daily, reproduction is almost prevented, but the female is more affected than the male (2). The former experiences a postparturient heat; the gestation period is 21 days; males are sexually mature at 6 to 8 weeks of age, and the females at 3 weeks (3). The average litter size in the laboratory is 3.73, and the sex ratio at birth is 50.89 ± 2.22 per cent males (4).

Wild field mice caught in Wales evidently reach puberty, both males and females, at between 12 and 20 g. in weight. Young of both sexes breed during their first season if they are born early enough. The winter anestrum is accompanied by closure of the vagina in the female and by cessation of spermatogenesis in the male. Spermatozoa appear about a month before any pregnant females are found. If the female does not become pregnant at the postparturient heat, lactation anestrum sets in. The vaginal and uterine changes are similar to those found in the house mouse. At copulation a hard vaginal plug is formed. The average number of corpora lutea found was $5.5 \pm .13$, standard deviation 1.5, and embryos $4.9 \pm .12$, standard deviation 1.37 (5).

1. Baker, J. R., and R. M. Ranson. Proc. Roy. Soc., London, 113B: 486–495, 1933.
2. Baker, J. R., and R. M. Ranson. Proc. Roy. Soc., London, 110B: 313–322, 1932.
3. Ranson, R. M. J. Anim. Ecol., 3: 70–76, 1934.
4. Ranson, R. M. Proc. Zool. Soc., London, 111A: 45–57, 1941.
5. Brambell, F. W. R., and K. Hall. Proc. Zool. Soc., London, 109A: 133–138, 1939–40.

Microtus guentheri Danforth and Alston

In captivity this Asiatic vole experiences no vaginal cycle with cornification, but the injection of estrogens has been found to induce cornification. Pregnancy urine has no effect upon the ovaries, and P.M.S. always causes follicle growth without luteinization. Anterior pituitary extracts produce both (1).

1. Zondek, B., and F. Sulman. Proc. Soc. Exp. Biol. and Med., 43: 86–88, 1940.

Microtus pennsylvanicus Ord

FIELD MOUSE

This field mouse is polyestrous and breeds all the year round in the laboratory. In the wild it tends not to breed in the winter except in the south or in warm conditions. The females reach puberty and begin to breed at 25 days of age; the males at 45 days. In captivity they begin to breed before they are half-grown. At first they have litters of 4, but later the more usual number

is 6 to 8. A female can have as many as 17 litters in one year (1). In a series taken in the wild the average number of embryos was 5.4, which represented 85 per cent of the eggs shed. Recognizable fetal resorption occurred to the extent of 3.6 per cent of the embryos, the modal number of which was 5. Combination of these data with another series (2) gives the following figures for fetal litter size: mean $5.5 \pm .05$, standard deviation 1.55, mode 5, range 1 to 11.

The ovaries are enclosed in a capsule, and the corpora lutea are salmon-colored. The vulva perforates at the first heat and is closed between heats. The clitoris is prominent. Copulation is rapid, and a vaginal plug is formed which lasts for 2 days. Copulation will take place immediately after parturition, and suckling does not lengthen the consequent gestation, which lasts 21 days or a little less. Low temperature alone does not interfere with breeding in winter (3).

During heat the vaginal epithelium cornifies, and the copulation plug is lined with cells of this type, which break away from the wall. Changes in the smear are typical of the rat and mouse, and leucocytes invade the vagina soon after the end of heat. Corpus luteum formation is typical, but the amount of liquor folliculi which is retained seems to be unusually large (4).

The male has a well-defined scrotum, but the testes are often partly retracted. The seminal vesicles are large and directed cephalad for two thirds of their length, then they turn ventrally and caudally. The prostate is large and compound, with well-marked lobes. The bulbo-urethral glands are small and somewhat pear-shaped. Preputial glands are present, but small (3).

1. Bailey, V. J. Agric. Res., 27: 523–536, 1924.
2. Goin, O. B. J. Mammalogy, 24: 212–223, 1943.
3. Hamilton, W. J., Jr. Cornell Univ., Agric. Exp. Sta., Mem. 237, 1941.
4. Asdell, S. A., and W. J. Hamilton, Jr. Unpublished work.

Ondatra zibethica L.

MUSKRAT

The muskrat of North America breeds in Iowa from April to August, or later (1). In Maryland it breeds at any time except possibly in November

and December, but most young are born from mid-April to mid-September. Two litters a year are usually obtained from pen-raised animals (2). The average litter size is 6.5, and it does not vary much with the season. The muskrat appears to breed first at the age of 1 year (1). The litter size varies from 1 to 11, and the sex ratio of the newly born is 58.1 per cent males (3). The period of gestation is probably 29 to 30 days (2).

Spermatogenesis begins in mid-December and ovulation in mid-February. Gonadal activity ceases in both sexes in late October. These facts refer to the muskrat in Maryland (4).

1. Errington, P. L. J. Wildlife Management, 5: 68–89, 1941.
2. Smith, F. R. U.S.D.A., Circ. 474, 1938.
3. Errington, P. L. J. Mammalogy, 20: 465–478, 1939.
4. Forbes, T. R. Science, 95: 382–383, 1942.

Other MICROTINAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Arvicola terrestris L.	Polyestrous (Didier et Rode)	2–7	42 days (?)	Europe and Asia
Clethrionomys (Evotomys) californicus Merriam	Polyestrous, May–Oct. (McNab and Dirks)	2–4		Western N. America
C. dawsoni Merriam		4–6		
C. nivarius Bailey	Polyestrous; postparturient heat	3.3	18 days	
C. skomerensis Barrett-Hamilton		5		Skomer Island, Wales. 1 record
Eothenomys fidelis Hinton		3, 3, 2		East Asia. 3 records
E. melanogaster Milne-Edwards		1, 2		East Asia. 2 records

Other MICROTINAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Lagurus curtatus Cope Pygmy Vole		6		Western U.S.
L. pauperrimus Cooper Sage Mouse		4–10, usually 5–7		Western U.S.
Lemmus trimucronatus Richardson		4–6		N. Canada
Microtus arvalis Pallas Field Mouse	Polyestrous, Feb.–Oct. (Didier et Rode)	4–7, usually 5–6	20 days	Europe
M. aztecus Allen Aztec Meadow Mouse	Polyestrous (N.A.F. 53)			Southwestern U.S.
M. blythi Blanford Blyth's Vole		6		India. 1 record
M. californicus Peale Californian Meadow Mouse	Polyestrous, almost all year (N.A.F. 55)	4–8	20–22 days	California. Puberty, males 6 weeks, females 20–22 days
M. chrotorrhinus Miller Rock Vole	Early spring to mid-fall (Hamilton)	$3.56 \pm .19$, usually 3–4		Northeastern N. America (Coventry)
M. ludovicianus Bailey Louisiana Vole	Late March–Oct. (Hamilton)	2–5		
M. mexicanus Saussure	Polyestrous (N.A.F. 53)	2–5		Mexico
M. minor Merriam	Polyestrous, late Apr.–late Aug. (Criddle)	1–8, usually 6		North-central N. America

Other MICROTINAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
M. montanus Peale Peale's Meadow Mouse	Polyestrous, spring–fall (N.A.F. 55)	4–8		Western N. America. Females, puberty 21 days
M. mordax Merriam Rocky Mountain Meadow Mouse	Polyestrous, May–Sept. (Long)	2–8, usually 4–5. $4.1 \pm .3$		Western N. America
M. nanus Merriam Dwarf Meadow Mouse	Polyestrous (N.A.F. 55)	4–10		Western N. America
M. nesophilus Bailey Gull Island Meadow Mouse	Late March–Nov. (Hamilton)	3–10	21 days	
M. nivalis Martin	Polyestrous (Didier et Rode)	3–4		W. Europe
M. ochrogaster Wagner	Polyestrous (N.A.F. 49)	3–7		Central N. America
M. operarius Nelson		5		Alaska. 1 record
M. oregoni Bachman Oregon Creeping Mouse	Polyestrous, May–Aug., at least (Svihla)	3–5		Oregon
M. richardsoni DeKay Water Vole		4–7		Northwestern N. America
M. sikkimensis Hodgson Sikkim Vole		3–4		N. India
M. townsendii Bachman Townsend's Vole		5		British Columbia to Oregon. 1 record

Other MICROTINAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Neofiber alleni True Round-tailed Muskrat	Probably all year (Hamilton)			N. America
Ondatra rivalicia Bangs Louisiana Muskrat	All year, mostly Nov.–Apr.	1–6, mode 4, av. 3.7		Louisiana (Svihla and Svihla)
Phenacomys intermedius Merriam Mountain Lemming	Polyestrous, Apr.–Aug. (Wallace)	4–6		Western N. America
P. longicaudus True Tree Mouse	Polyestrous, all year, mainly early spring to late summer (Benson and Borrell)	1–3, usually 3		Western N. America
P. olympicus Elliot		4		Washington. 1 record
P. sylvicola Howell		4		Oregon. 1 record
Pitymys nemoralis Bailey Pine Mouse		2		Central N. America. 1 record
P. pinetorum Le Conte Pine Mouse	Early Mar. to mid-Nov. (Hamilton)	Usually 2–3, $2.9 \pm .15$		
Synaptomys cooperi Baird Lemming Mouse	Polyestrous, Feb.–Nov. (Stegeman)	1–5 $3.2 \pm .19$		N. America
S. helaletes Merriam		4, 5		N. America. 2 records

GERBILLINAE

Dipodillus simoni Lataste

GERBIL

This gerbil from Algeria is polyestrous and breeds all the year. The female usually comes in heat during the afternoon or evening and is out of heat next morning. The cycle is said to last about 10 days. A vaginal plug is formed after copulation. Gestation lasts 20 to 21 days, usually 20. The mean litter size is 4.7, with a range of 1 to 7 (1). If the female is suckling and becomes pregnant, implantation of the embryos is delayed (2). More information is needed on this species since the records of a 10-day cycle were made at a time when pseudopregnancy had not been recognized. The cycle in the unmated gerbil may be shorter. These remarks also apply to other species of gerbils investigated by Lataste.

1. Lataste, F. Act. de la Soc. Linn. de Bordeaux, 40: 295–460, 1886.
2. Lataste, F. Compt. Rend. Soc. Biol., Paris, 43: 21–31, 1891.

Pachyuromys duprasi Lataste

BOUBIÉDA

This North African gerbil is polyestrous. After copulation a vaginal plug is formed with cornified tissue around it. The gestation period is 19 to 22 days, usually 20. The number of young is 3 to 6, mean 3.4, mode 3 (1).

1. Lataste, F. Act. de la Soc. Linn. de Bordeaux, 40: 295–460, 1886.

Other GERBILLINAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Desmodillus auricularis A. Smith Short-eared Gerbil	Probably polyestrous (Powell)	2–6		S. Africa
Dipodillus campestris Levaillant	Polyestrous, cycle about 10 days (Lataste)			Algeria
D. quadrimaculatus Lataste		4		Egypt. 1 record
Gerbillus hirtipes Lataste	Polyestrous, cycle about 10 days (Lataste)			Tunis
G. swalius Thomas and Hinton Damara Pygmy Gerbil	Fetuses found Oct.–Dec., Apr. (Shortridge)	2–6		S.W. Africa
Meriones libycus Lichtenstein Jird	Polyestrous, cycle about 10 days (Lataste)		20–25 days	N. Africa. Delayed implantation if suckling (Lataste)
M. longifrons Sand Rat	Polyestrous, cycle about 10 days (Lataste)		21 days	S. Europe. Delayed implantation if suckling (Lataste)
Psammomys obesus Cretzschmar	Born Apr. (Anderson)	3–5		N. Africa and W. Asia
Tatera indicus Hardwicke Antelope Rat		8–12		India
T. schinzi Noack Schinz's Gerbil	All year, mostly spring and summer	2–8, mode 4–5		S.W. Africa. Puberty at 3 months (Powell)
T. validus Bocage Large Gerbil	Born Apr.	5		Angola. 1 record
T. vicina Peters	Fetuses found Nov. and Dec. (Heller)	4, 5		Cent. Africa. 2 records

OTOMYINAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	HABITAT, ETC.
Otomys irroratus Brants	Polyestrous, all year, mainly June–Aug.	2–5, usually 2–3	S. Africa. Puberty at 3 months (Powell)
Parotomys brantsii A. Smith	Polyestrous		S. Africa. Puberty at 3 months (Powell)
P. littledalei Thomas	Aug., Nov. (Shortridge)	3	S. Africa

DENDROMURINAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	HABITAT, ETC.
Dendromus (*Poemys*) *acraeus* Wroughton	Embryos in July (Hollister)	3	Kenya. 1 record
D. (*P.*) *arenarius* Roberts Gray Tree Mouse	Winter (Roberts)	3–4	S. Africa
D. (*P.*) *ochropus* Osgood Chestnut Tree Mouse	Embryos in Jan. (Hollister)	5	E. Africa. 1 record
Malacothrix typicus A. Smith Mouse Gerbil	Probably polyestrous	3–5	S. Africa. Puberty at 3 months (Powell)
Petromyscus collinus Thomas and Hinton Damara Pygmy Rock Mouse	Embryos Sept. (Shortridge)	2	S.W. Africa. 1 record
P. shortridgei Thomas Kaokaveld Pygmy Rock Mouse	May (Shortridge)	2–3	S.W. Africa

DENDROMURINAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	HABITAT, ETC.
Saccostomus anderssoni De Winton Pouched Mouse	Embryos Dec. (S.W. Africa), July (E. Africa) (Shortridge, Heller)	4–8	Central S. Africa
Steatomys pratensis Peters Fat Mouse		4–6	Cent. and S.W. Africa

RHIZOMYIDAE

SPECIES	NO. OF YOUNG	HABITAT, ETC.
Rhizomys pruinosus Blyth Hoary Bamboo Rat	3–4	W. Asia

MURIDAE

MURINAE

Mastomys coucha A. Smith

MULTIMAMMATE RAT

A subspecies (*M. c. erythroleucus* Temminck) of the multimammate rat from Sierra Leone has been investigated. It is polyestrous and breeds at all times of the year, but most females are found pregnant in October and November, at the end of the rainy season. At any other time of the year some females may be in anestrum, but the males breed at any time. At puberty the

males weight 45 g., and the females 40 g., compared with their respective mature weights of 105 g. and 83 g. Ovulation is spontaneous, and there is a postparturient heat. If the female does not become pregnant at this time, a lactation anestrum sets in. A vaginal plug is formed after copulation. The uterus is filled with fluid during heat, but this is not so at the postparturient heat. The vaginal epithelium becomes intensely mucified during proestrum. During heat it becomes cornified below the layer of mucous cells, and in metestrum both layers are sloughed off. The mean litter size is 11.5 by embryo counts, with a range from 7 to 17. The number of corpora lutea is 12.1, with a range from 5 to 19 (1).

The age at puberty is 3 months (2). In the North Cameroons pregnant females were found only from October to December (3).

1. Brambell, F. W. R., and D. H. S. Davis. Proc. Zool. Soc., London, 111B: 1–11, 1941.
2. Powell, W. Rodents. Dept. of Public Health, Union of South Africa, 1925.
3. Sanderson, I. T. Trans. Zool. Soc., London, 24: 623–725, 1938–40.

Mus bactrianus Blyth

PERSIAN HOUSE MOUSE

This Asiatic mouse when kept in the laboratory is polyestrous and breeds all the year round. It experiences a postparturient heat. The mean age at which the female gives birth to her first litter is 177 ± 6.2 days. Gestation lasts 20 days if the female is not suckling. The mean litter size is $4.4 \pm .09$ (1).

1. Green, C. V. J. Mammalogy, 13: 45–47, 1932.

Mus musculus L.

HOUSE MOUSE

The house mouse is polyestrous all the year round, and in all respects its reproductive cycles closely resemble those of the rat. As the cycle has been described in detail under that species, reference should be made to it there.

The age of establishment of the vaginal orifice is somewhat variable. One investigation gave a spread from 28 to 49 days, a mean of $35.5 \pm .3$ days, and a standard deviation of 4.75 days. In this investigation the weight at opening gave a slightly closer fit than age. The mean weight was $13.15 \pm .08$ g. (1). Temperature has some effect on the time of opening. In mice raised at 60 to 64° F. cycles began at 30.8 days, while in those raised at 80 to 92° F. they began at 34.2 days (2). There was no difference between mice kept in total darkness, in darkness with 1 hour of light daily, with red light, or kept normally (3). The vagina opens 1.4 days before the onset of the first heat (4).

The length of the estrous cycle varies from 3 to 9 days, with an average at 4.5 days, and a mode from 4 to 6 days. However, the length appears to vary with the color of the mouse. Brown mice have the longest cycles, a modal length of 5 to 6 days; grays and yellows, 5 days; blacks, 4 days; and albino "browns," 4 days. Most of the prolongation was in the duration of heat (5). A small decrease in environmental temperature has no marked effect upon the duration of cycles, but a reduction to 0° C. increases the interval from $4.02 \pm .14$ to $11.16 \pm .59$ days. After one week at the lower temperature the cycle is restored to its normal length (6). The onset of heat, as judged by willingness to mate, usually occurs between 10 P.M. and 1 A.M. The spontaneous ovulation is usually between 12 midnight and 2 to 3 A.M., and the spread is from 11:30 P.M. to 4:40 A.M. It occurs, therefore, about 2 to 3 hours from the onset of heat, but the interval is variable. If mice are submitted to a reversal of the time of light, and are also subjected to 16 to 17 hours of light, the onset of the first heat is accelerated and they mate at the time customary under usual light conditions, i.e., in the dark hours (7). Mating has no effect on the time of ovulation. The first polar body is nearly always extruded between the onset of heat and ovulation. At the time of first acceptance of the male the vaginal smear consists of from 21 to 95 per cent cornified cells (8).

The mouse requires a sterile copulation or stimulation of the cervix uteri to activate the corpus luteum in the absence of fertile copulation, and then she displays the phenomenon of pseudopregnancy which lasts for 10 to 12 days (9).

Heat and ovulation occur within 24 hours after parturition. If the female is allowed a sterile copulation at that time, the ensuing pseudopregnancy is prolonged to 21 to 29 days if she is suckling. In nonsuckling animals and in those suckling only 1 or 2 young this prolongation is not observed (9).

The ova take 3 days to traverse the oviduct and remain for 1 day in the last portion of the tube (10).

The litter size in mice has been the subject of many papers (11,12). The means reported vary from 4.5 to 7.4. The second litter is the largest, and there is a steady decrease afterwards so that the sixth litter averages less than the first (12). Fertility rises slightly through the year to July and September. Litters during lactation tend to be 0.3 lower than those born when the mother is not lactating (13). Counts of corpora lutea, embryos, and young born have averaged 8.4, 6.35, and 5.86, respectively, showing the considerable loss which occurs from ovulation to birth, due to loss of eggs, failure of implantation, and fetal resorption. The embryos are distributed about equally between the two uteri, but there are too many occurring all on one side, because of pathology of one oviduct (14). If uniovular twins occur they must be infrequent, less than 0.7 per cent (15). The sex ratio is about 52 per cent males (16), and the duration of gestation is 19 days, varying from 18 to 20. If the female is suckling at the time, implantation is delayed, and gestation is prolonged, on the average, by 21 hours for each suckling young (17). Most births take place from 4 P.M. to 4 A.M., and the fewest from 4 A.M. to 8 A.M. The female remains in seclusion an average of 4 hours and 40 minutes, during which time the litter is born (18).

HISTOLOGY OF THE FEMALE TRACT

OVARY. At every heat period an average of 400 to 500 young ova in each ovary differentiate, but most are destined for atresia. Semispaying does not increase the number differentiating, but it does increase the number that mature, thus giving the normal number of ovulations from one ovary instead of from two (19). The graafian follicles measure about 0.4 mm. in diameter 2 days before heat, when they begin their rapid ripening growth. They measure about 0.7 mm. when ovulation occurs (20). After rupture of the follicle the granulosa cells mostly remain and hypertrophy to form the lutein cells. The spindle cells of the theca interna and externa divide by mitosis to form connective tissue strands. Theca interna cells do not enter into the formation of lutein cells, but polygonal cells are formed from them, which, however, degenerate within 60 hours of ovulation (21).

New ova are produced from the germinal epithelium, and most mitoses are found in this layer immediately following ovulation (22). The injection of

estrogens during the diestrous period causes mitoses to occur during that time, when normally there are few (23). Follicular atresia varies in a cyclical manner; it is highest the day after heat and lowest on the next day (24). A count made in 100 ovaries revealed 2 polynuclear ova, 16 binovular and 2 triovular follicles, and 13 anovular follicles, which were in an advanced stage of atresia (25). The average diameter of the ovum is 78.4 μ or, with the zona pellucida, 95.4 μ (26).

VAGINA, etc. The vagina and vaginal smears are similar to those found in the rat. By the use of colchicine and estrogens in the ovariectomized mouse it has been shown that growth of the vaginal epithelium starts at the uterine end and proceeds toward the vulva (27).

The uterine changes are also similar to those in the rat. There is a heavy leucocytic infiltration of the endometrium just after heat (28).

The ciliated and nonciliated cells of the oviduct secrete and show maximal activity during heat. Eosinophil lipids are formed during diestrum and are secreted during estrus (29).

PHYSIOLOGY OF THE FEMALE TRACT

The ovary of the mouse seems to have remarkable powers of regeneration, since in 121 mice doubly ovariectomized with the removal of the capsules and parts of the oviducts all ceased to experience cycles at first, but later 11 of them came into heat. Of these, 8 were found to have ovarian tissue with follicles and corpora lutea (30). The injection of anterior pituitary extract did not increase the percentage of recovery (31). The role of the ovary in maintaining estrous cycles has been questioned, as it was found that X-ray sterilization before puberty, with oöcytes, follicles, and follicular tissue all apparently rendered nonfunctional, did not prevent most of the mice from having estrous cycles. The tubular genitalia remained normal (32). When the experiment was repeated with adult mice, the average length of cycles was increased to 6.0 to 6.6 days, but it became more variable (33). Perhaps these experiments should be considered in conjunction with the preceding in which regeneration after ovariectomy was recorded, though they have recently been used as evidence for the secretion of estrogens by tissues other than the granulosa cells.

It is believed that the graafian follicles secrete sufficient estrogen to induce heat early in their growth since ovariectomy 36 to 48 hours before heat does not prevent its occurrence at the usual time (34).

If 0.04 to 0.06 R.U. of estrogen is injected into mice, i.e., considerably less than the amount needed for cornification, the vaginal epithelium is converted into a mucus-secreting type (35). The same effect can be brought about if progesterone is injected together with a cornifying amount of estrogen (36).

Deciduomata can be produced by traumatization of the endometrium during pseudopregnancy. The reaction is strongest at 3 to 4 days and slight at 5 to 6 days. They can also be evoked, but not so strongly, in a pseudopregnancy which is concurrent with lactation. They cannot be produced after X-ray sterilization, or after X-ray treatment and the injection of anterior pituitary extract to cause luteinization (37). Removal of the ovaries at any time during pregnancy causes resorption of the embryos or abortion (38,39). Hypophysectomy at mid-pregnancy does not cause the pregnancy to end (40).

Pregnancy cells appear in the anterior pituitary of the mouse at the appropriate time. The reaction depends upon the ovary, as the injection of anterior pituitary extract can produce the effect, but only in the intact animal. It can also be produced in males by injection if ovaries have been transplanted into them. In other words the reaction is dependent upon the presence of corpora lutea (41). During pregnancy there is a leakage of red blood cells from the placenta, known as the placental sign, which can be detected in the vaginal smear from 9 to 10 days (42). Ovariectomy 1 to 12 hours after the vaginal plug has been formed locks the eggs in the oviduct. One injection of 200 R.U. of estrogen is sufficient to repair the damage to the tubes and allow the eggs to descend (43).

The pH of the uterine fluid at different stages of the cycle are as follows (44):

Stage I	6.97
" II	7.13
" III	7.50
" IV (diestrum)	7.20

These figures are all about 0.2 units below the corresponding ones in the rat.

The uterine muscle is slightly more responsive to oxytocin during heat than between heats, and the response during pseudopregnancy is comparatively low, just as it is during pregnancy (45).

The mouse unit of estrogen is often used as a measure, but it varies with the laboratory from 0.2 to 1.0 of a rat unit. This variation may either be caused by differences in the method of testing or by strain differences. It should be

valuable if several strains could be tested by a standardized technique and the results expressed in international units. If there is a great difference between strains, an inquiry into the mode of inheritance might yield valuable results. There is also a seasonal difference, since the response to 1 I.U. is three times as great in May as it is in November (46). If estrogen and progesterone are injected in sequence, sexual receptivity is more easily produced in the ovariectomized mouse than it is if estrogens alone are injected. The optimal amount of progesterone is 0.05 I.U., and the optimal interval is 48 hours (47). The pregnant mouse produces about 1.5 mg. (= 1.5 Rab.U) of progesterone daily, according to the method of estrogen neutralization (48). The adult female's pituitary contains 0.25 B.U. of prolactin per mg. of tissue (49).

The ovaries of immature mice do not respond to pituitary implants until the mice are 15 days of age (50). After this age, but while they are still immature, 2.5 I.U. of P.M.S., or 1.5 I.U. of P.U., are needed to cause ovulation. During pregnancy it may be induced by 0.7 I.U. of P.U., but in diestrum 1.0 I.U. is required (51). Hysterectomy reduces the response to threshold doses of chorionic gonadotrophin in 20-day-old mice (52). Prolactin injected into the female suspends cycles for 3 weeks; then a prolonged estrus of 4 to 8 days occurs in spite of continued injections (53).

The minimal dose of estrogen that will produce uterine distension is 100 M.U. (divided into 4 injections given over a period of 36 hours), but distension did not occur in all cases until the dose was raised to 400 M.U. At over 100 M.U. copulation was induced in 50 per cent of cases (54). The injection of 500 M.U. produced overstimulation of the uterus, and greatly distended glands, with a Swiss-cheese effect, were observed (55). In the normal cycle the injection of 7.5 R.U. of estrogen when the eggs are in the tube causes them to be retained or "tube-locked" (56). Similar effects are produced by testosterone propionate, 0.5 mg. of which causes some delay in the passage of ova, while 2.0 mg. completely prevents it (57). One to three M.U. of estrogen induces estrous vaginal smears in mice pregnant 2 to 6 days, with resorption of the embryos. The same effect with resorption or abortion is caused by the injection of 2 to 2.5 M.U. between 4 and 10 days. After 11 days 3.0 M.U. or more are needed (42). In the pregnant mouse ovariectomized at 14 to 15 days, 1.0 mg. of progesterone daily is needed to maintain the pregnancy (58). The daily amount of progesterone needed to sensitize the endometrium to produce deciduomata on traumatization lies between 0.25 and 0.5 mg. (59). In normal pseudopregnancy deciduomata produced on the third day persist for 5 days. If 1 mg. of progesterone daily

is injected subcutaneously for a period beginning within 3 days of traumatization, they survive for 10 days, but not longer even though the injections are continued. The same effect can be produced in ovariectomized females. The additional injection of estrogens or of androgens do not affect the survival time (60).

The X-zone or zone of fuchsinophil cells has been observed in the adrenal cortex. The injection of 0.4 mg. of testosterone propionate daily causes it to disappear or prevents its formation in adolescent males and females, adult females, and in adult castrated males (61).

Estrous cycles are suppressed by the daily injection of 20 μg. of testosterone and also of 200 μg. of progesterone (62).

The prenatal growth of the mouse has been studied in detail, and tables of growth have been prepared (63).

THE MALE

In the developing male the seminal vesicles increase in weight most rapidly at a body weight from 19 to 24 g. If postpuberal castration is performed, they lose half their weight in 7 days and then gradually sink to a level of less than 10 per cent of their maximal weight (64). The accessory glands are maintained in castrated males if ovaries are implanted into the ears and the mice are then kept at a temperature of 22° C. If the environmental temperature is 33° C., they are not maintained. The inference has been drawn that androgens are secreted by ovaries maintained at the lower temperature (65).

The fertile life of spermatozoa in the male tract is about 10 to 14 days, since fertility is retained for that period after spermatogenesis is halted by X-raying the testes (66). Spermatozoa enter the oviducts 1¼ hours after copulation and meet the ova at the end of 2 hours. In the oviducts spermatozoa retain their fertilizing ability for 6 hours and their motility for 13½ hours. The presence of a copulation plug is not necessary for fertilization (67). The plug seals better than does that of the rat. It extends up each cervical canal and into the vulva; the end is flat, not pointed as in the rat, and usually flush with the vulva. The plug is removed by softening at the surface. It usually falls out after 18 to 24 hours, though it may persist for 36 hours to 2 days. The plug formed at a postpartum copulation is not so definite owing to a copious discharge of fluid and leucocytes. Under these circumstances the plug either does not form or breaks into a mass of debris (9).

Two milligrams of androsterone daily is just insufficient completely to

maintain the prostate and seminal vesicles of castrated mice, which fact indicates that the mouse requires more than the rat (68). The minimum daily dose of testosterone that will bring the castrated mouse into a condition in which ejaculation can occur when pernostone and yohimbine are injected is about 40 γ (69).

The injection of crystalline androgens prevents the degeneration of the seminiferous tubules in hypophysectomized males for at least 23 days, but it does not prevent the degeneration of the interstitial cells. Androstanedione was most effective in a dose of 0.4 mg. daily (70). Injection of larger quantities is harmful in the normal adult mouse. Two milligrams of testosterone daily for 20 days produced moderate tubal atrophy and more complete atrophy of the interstitial cells. Five to ten milligrams daily did not damage the seminiferous tubules, but atrophy of the interstitial cells occurred. The injection of 2 mg. of progesterone also caused atrophy of the interstitial cells (71). Estrogens in quantity are also harmful to the male; 40 R.U. daily decreased the weight of the prostate (also of the uterus in the female) and caused the retention of urine and bladder dilatation in both the intact and the castrated male. Metaplasia of the columnar epithelium into stratified squamous epithelium occurred, and it was more marked in the anterior than in the posterior prostatic lobe. The effect was greater in castrates than in intact mice. Injection of P.U. and of androgens prevented the metaplasia but not the retention of urine (72).

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Rattus rattus L.

RAT

The nomenclature of the species and subspecies of rats is in a very confused state, and in this account no attempt has been made to differentiate between them. Laboratory rats, whatever their origin, have, unless specifically stated, been taken to belong to one species. The basic physiology in all is the same, but there are differences in quantitative aspects, such as the age at puberty and mean litter size, comparable to similar variations found in farm livestock. We are probably witnessing in the laboratory rat that blending of species and subspecies with subsequent genetic separations into strains which has produced domestic livestock and the many breeds into which they are now separated.

The rat is polyestrous all the year round, and ovulation is spontaneous, occurring near the end of heat. Heat lasts about 20 hours, and the cycle from 4 to 6 days. The corpus luteum formed after rupture of the follicle is physiologically inactive unless the cervix uteri has been stimulated mechanically or by coitus. The interval between heats thus represents proestrum, and its length is determined by the time required to ripen new follicles. When the cervix is stimulated, prolactin is apparently released from the anterior pituitary and this enables the corpus luteum to secrete progesterone. This con-

tinues for about 14 days, and during that time the rat is "pseudopregnant." New follicles do not ripen, heat is not experienced, and the uterus undergoes various changes, such as growth of the glands and sensitization of the endometrium to trauma. Subsidence of the corpora lutea is followed by the ripening of new follicles, heat, and ovulation.

The vaginal epithelium undergoes well-marked changes during the cycle. Heat is characterized by marked cornification and the disappearance of leucocytes. At the end of heat the cornified layer is sloughed off, and an invasion of leucocytes occurs. The vaginal smear is, therefore, an excellent indicator of the stage of the cycle. The uterine lumen is distended with fluid at heat, but otherwise uterine changes are not marked in either type of cycle. The duration of gestation is about 21 days, and the average litter size 7 to 9. Quantitative hormonal relationships have been worked out in considerable detail.

THE ESTROUS CYCLE

In the young rat the vagina is a cord of cells without a lumen. As the first ovulation approaches, the central cells separate, forming a tube closed at the vaginal orifice by a thin membrane. This ruptures at, or a little before, the first ovulation; hence, the establishment of the opening is a good indication of the arrival of puberty. Opening is not, however, entirely dependent on sexual activity as it occurs in the absence of the ovaries at about the usual time in the Long-Evans strain (1). In the Cornell Nutrition strain ovariectomy delays the opening for about 14 days (2).

TABLE 1. Age and Weight of Rats at Time of Vaginal Opening

STRAIN	AGE, DAYS	WEIGHT, GRAMS
Columbia Univ., specially fed (3)	$41.1 \pm .45$	127.0 ± 1.3
Wistar (4)	$42.0 \pm .7$	87.8 ± 1.6
Hooded (4)	46.5 ± 1.3	91.0 ± 2.3
Brown Univ. (5)	$49.4 \pm .26$	———
McCarrison (4)	50.6 ± 1.7	96.8 ± 1.8
Cornell Nutrition (2)	$60.8 \pm .6$	120.8 ± 2.8
Long-Evans (1)	76.5	———

The average age at puberty varies considerably with the strain of rats and with the rate of growth. Rats from small litters and those which are specially fed reach this age earlier than others (3). The mean weight at this

time is about 52.5 per cent of the mature weight, but, as the coefficient of variation for weight is greater than that for age, the latter is more closely related to the attainment of puberty (2). However, the body length, mean, $166.0 \pm .6$ mm., is still less variable (3). Another series of data, also, gives 148 to 150 mm. as the body length at puberty or first appearance of corpora lutea, and it seems that this is the less variable measurement (6).

The opening of the vagina and ovulation are practically simultaneous in 46 per cent of rats, and they have occurred within 10 days of each other in 80 per cent. If males are with the females all the time, the first fertile copulation occurs, on the average, about 16 days later than vaginal opening in the Long-Evans strain (1), and 6 days later in the Cornell Nutrition strain (2).

The modal length of the estrous cycle in the Long-Evans strain is 4 to 5 days, with 82 per cent of all cases falling between 4 and 6 days. The average of all cases 8 days and less in length was 4.8 days, and this may be taken as the mean since periods longer than 8 days may include some rats one of whose heat periods has been missed (1). The Stanford colony gave a mode of 4 days for rats of all ages, though the mean for older rats (above 283 days old) was about 1 day longer than that for young ones because of the greater irregularity of the former (7). The Brown University colony gave a mean of 4.4 days, with 87 per cent between 4 and 6 days. Occasional split heats were observed (8). In South Africa the modal cycle length for albino rats was 4 days, with 80 per cent from 3 to 5 days (9). It is thus generally agreed that the modal length of the cycle is 4 days and the mean about 4.8 days.

The length of the pseudopregnant cycle after electrical stimulation of the cervix is 14.03 days (10), and after vasectomized copulation, 14.5 days (11). The difference is probably not significant. The mode in the first report cited was 12 to 13 days. In the Long-Evans strain the modal length was 12 to 14 days (1). Pseudopregnancy is also induced by the application of silver nitrate solution to the nasal mucosa during heat (12). Anesthetization of the nasal mucosa and also ablation of the sphenopalatine ganglia have a similar effect (13). Bilateral abdominal sympathectomy does not affect the normal cycle (14) or the induction of pseudopregnancy after infertile copulation, but it does prevent pseudopregnancy from following mechanical or electrical stimulation of the cervix. In the latter, therefore, the sympathetic chain is involved (15).

The duration of heat has been determined by hourly copulation tests. This method gave $13.7 \pm .12$ hours, with a range of 1 to 28 hours and a

standard deviation of 4.55 hours. Eighty per cent were between 9 and 20 hours. Copulation early in heat shortens the period slightly (8). Another determination gave a distribution from 12 to 18 hours (16). Heat usually begins between 7 and 8 P.M., with 75 per cent beginning between 4 P.M. and 10 P.M. and less than 1 per cent between 3 A.M. and 11 A.M. (8,16). The average duration of the first heat is slightly less than that of later heats, the mean being 9.1 hours. It usually begins between 7 P.M. and 5 A.M. (5). In the normal heat period the female is most receptive during the first 3 hours (16). The usual time of ovulation is 8 to 11 hours after the beginning of heat (17,18). The relation of ovulation to the vaginal smear is considered later.

As the rat is a more or less nocturnal breeder, the influence of light upon the reproductive processes is of interest. Rats kept from birth or from 21 days of age in continuous light experienced the vaginal opening at an average of 6 days earlier than controls, while those kept in continuous darkness were 10 days late. In light the heat period was longer, and in darkness the interval between heats was longer, than usual (19). Reversal of the hours of light and darkness, but with their relative lengths retained, caused a shift of the onset of heat to the new time of darkness. Establishment of an 8-hour rhythm of light and darkness had no effect, and exposure to constant light increased the length of the heat period and the duration of vaginal cornification (20,21). Blindness and continuous darkness did not affect the cycle (21).

The removal of active corpora lutea during pseudopregnancy results in a return of heat in 4 days' time. If it is done late in pregnancy, abortion sometimes occurs, more often resorption of the embryos, and occasionally the pregnancy is not interrupted (22). Ovariectomy, a less severe operation, apparently, than removal of corpora lutea by electrocautery, results in abortion if it is done before 13 days of pregnancy; if it is done later, the pregnancy continues (23).

Parturition usually occurs in the afternoon, least frequently from midnight to 6 A.M. It takes from 10 to 70 minutes. The postparturition heat begins after a mean interval of 18.5 hours (range 4 to 36 hours). The time of its commencement is somewhat irregular, but it is related to the time of parturition in such a way as to bring it between 6 P.M. and midnight, the usual time for heat to begin. The average length of this heat period is 10 hours. Occasionally ovulation occurs without heat after parturition (24).

There is little difference in the relative activity of the two ovaries. A count of corpora lutea gave 51 per cent of ovulations from the left ovary (6).

The results of insemination at different times in the cycle are given in the following table (25,26). This work sets the maximum fertile life of the spermatozoa in the female tract at 14 hours, and the life of the ovum at about 12 hours. But as the ova become old they are less able to give rise to normal embryos.

TABLE 2. Relation of Time of Insemination to Fertility and Fecundity

TIME OF INSEMINATION	PREGNANCIES, PER CENT	NORMAL PREGNANCIES, LITTER SIZE	ABNORMAL PREGNANCIES, PER CENT
More than 14 hours before ovulation	0	0	0
12–14 hours before ovulation	20	3.5	0
10–12 hours before ovulation	50	3.5	0
Near ovulation time	83	6.7	11
6 hours after ovulation	47	4.6	48
10 hours after ovulation	22	1.8	79
12 hours after ovulation	4	0	100
18–20 hours after ovulation	0	0	0

The rate of passage of the ovum through the oviduct appears to be rather rapid until the last tenth of the distance remains to be traversed, when it is much slower. The ovum takes 3 days or a little more to reach the uterus (27,1).

The mean litter size varies with the strain. Stock albino rats at the Wistar Institute averaged 6.1 (28); Wistar rats in Edinburgh, 9.26 ± .18 (29); albinos in South Africa, 7.4 (9); Cornell Nutrition strain, 6.22 ± .08 (30); wild rats brought into the laboratory, 10 to 11 (31). The second litter is the largest, and the litter size decreases sharply after the tenth litter (28,32). The litter size tends to be slightly smaller in fall and winter (9). Unilateral ovariectomy is followed by the production of the number of ova usual for the rat from the remaining ovary, so that the litter size falls only from 8.6 to 8.1, while the number of corpora lutea increases from 10.3 to 10.6. No migration of ova across the abdominal cavity occurs; the ova could not migrate through the uteri as the latter open to the vagina by two cervices. In these experiments, therefore, the pregnant uterus had twice the normal number of young in it with little increase in the amount of fetal atrophy

(33,34,35). In the normal rat loss of ova and fetal atrophy account for about one third of the eggs shed (1).

A comparison has been made of the effects of breeding rats at the earliest possible time, i.e., at the time of vaginal opening, at 100 days of age (normal time), and at 280 days old. In all these groups lactation for 21 days was allowed before the rats were rebred. A fourth group was not allowed to lactate: the young were removed immediately after parturition and the mother was put in a cage with a male. In all these groups the second litter was the largest; the "bred late" rats had the smallest litters throughout their lives; and the "bred early" rats had larger initial litters than the normals but ceased reproduction rather earlier than usual. The "nonlactating" rats had consistently larger litters after the first, and, though they had more litters, they tended to break down at an earlier age. The size of the first litter, and the shortness of the interval between the first and second litters in the lactating rats, was a fairly reliable indication of their lifetime ability to reproduce. The menopause, or cessation of breeding, was found to be a process which might occur at any age or not at all; no definite period for cessation, as in man, was found (32).

The sex ratio at birth in Wistar stock is 51.4 per cent males (28). This seems to be a characteristic ratio, since the same stock in Edinburgh has given a sex ratio of 51.2 per cent males (29). South African albino stock gave a ratio of fewer males than females, i.e., 43.4 per cent males (9), and the Cornell Nutrition stock, 49.4 per cent males (32).

The gestation period is 22 days with very little variation. A series in which the time was accurately obtained by the use of obstetrical cages gave 90 per cent from 21½ to 22 days, and the average of all gestations was 21.8 days (1).

If the mother is suckling 6 or more young, implantation in a new pregnancy is delayed, and the pregnancy is consequently prolonged (36). In the absence of pregnancy lactation causes the corpora lutea of the postparturition ovulation to persist. Removal of the young is followed by heat 4 days later (1).

HISTOLOGY OF THE FEMALE TRACT

OVARY. The ovary of the immature rat less than 15 days old contains ova surrounded by granulosa cells. These loosen and antra develop at about

15 days. At this time the percentage of vesicular follicles is about 12. It increases up to 38 days, then falls until just before puberty, when there is a sudden rapid increase (37). The fall may be due to the large amount of follicular atrophy. The number of binovular and triovular follicles is very small, about 0.05 per cent (38), which is in contrast to their relative frequency in the mouse. The number of ova of all sizes in the two ovaries at birth is about 35,000; at 100 days it has fallen to 8,000; at 400 to 600 days to 5,000; and at 950 days to about 2,000. At any one time degenerating ova account for 10 per cent of all those present (6).

Comparatively few mitoses are found in follicles below 200 μ in diameter, indicating a slow rate of growth up to this size (39). Follicles which are destined to rupture begin to grow at the previous heat of the 4-day cycle. The growth rate is fairly constant until just before heat when there is an 8-fold acceleration. Follicles which will not rupture but which are destined to become atretic can be picked out at the third day of the cycle (18). The greatest number of mitoses in the granulosa cells is found early between heats, and the volume of the theca interna is greatest just before the heat in which the follicles will rupture (39).

The first sign of impending ovulation is a slight indipping of the theca interna. As this occurs the first polar body is extruded, and some of the outermost granulosa cells have minute lipid deposits within them. At this time the follicle is about 0.9 mm. in diameter (1). The theca interna thins out at the point of rupture. When ovulation occurs, the follicle collapses; some of the granulosa cells and a little liquor folliculi are retained. A small crater forms at the rupture point, but it soon heals over, and the follicle again becomes somewhat distended by the secretion of more fluid (18). At 24 hours after ovulation a layer of lutein cells has been formed, and at 48 hours these cells are well developed. They surround a small core of connective tissue, which occasionally contains extravasated blood. The corpora lutea reach their maximum size, about 0.8 mm. in diameter, after 3 days, and retrogression sets in immediately (40), though they may be easily distinguished for three cycles (1). The corpora lutea of pregnancy last throughout gestation and retrogress slowly, and those of pseudopregnancy continue for 12 days and then slowly retrogress. The most apparent sign of retrogression is a reduction in the amount of lipid in the lutein cells (1). It has been stated that the mean maximum diameter of the corpus luteum of the normal cycle is 1.77 mm., of that of pseudopregnancy, 1.52 mm., and of that of lactation, 1.59 mm. The corpus luteum of pregnancy increases slowly to 1.45 mm. by

the eleventh day; then there is a rapid increase to 2.0 mm., at which size it remains until parturition. In the delayed implantation caused by lactation the secondary growth of the corpus luteum is also delayed. The increase can be brought about by the injection of estrogens, probably supplied normally by the placenta (41).

VAGINA. Vaginal changes in the rat are definitely related to the estrous cycle and are exceptionally clear-cut, so much so that the vaginal smear is an excellent means of determining the stage of the cycle. During metestrum the vaginal wall is moist and pinkish, but in estrus it is dry, white, and lusterless (1). These changes are associated with the cornification of the surface layers during heat and the extensive desquamation at the end of this period. It may be noted that these color changes are the opposite of those occurring in the domestic ungulates, but in these species not cornification but mucification is the rule in estrus. During the interval the epithelium is 4 to 7 cells deep with little squamous transformation of the surface layers and few mitoses in the basal layer. Leucocytic infiltration is always present. Toward the end of this period, i.e., during proestrum, mitoses are much more frequent and the epithelium increases to 8 to 9 layers. The surface cells swell and become a characteristic surface layer, while, with continued growth, those beneath become cornified. These two layers are gradually sloughed off during heat, and at the end of this period a heavy invasion of leucocytes appears. This is followed by the "interval" type of epithelium.

Along with these changes in the vaginal epithelium there are well-marked changes in the type of vaginal smear. In the interval nucleated epithelial cells and leucocytes, with an occasional cornified cell, are found. As heat approaches, the leucocytes disappear and nucleated epithelial cells increase in number and are gradually replaced by cornified nonnucleated cells. The beginning of heat (sexual receptivity) usually occurs when the smear contains 75 per cent nucleated and 25 per cent cornified cells. This is followed by a second stage in which cornified cells only are present. Gradually "pavement" cells come in. These are flat, nucleated epithelial cells. During the latter part of the cornified stage the smear becomes very abundant and cheesy in texture. Heat may end at any time during the cheesy stage. It is followed by the appearance of large numbers of leucocytes and the virtual disappearance of cornified cells. Two schemes denoting the stages of the vaginal smear of the rat have been given, and they are summarized in table 3.

UTERUS. The chief characteristic of the uterine changes is the marked distension with fluid which occurs during estrus. In diestrum the uterus is

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TABLE 3. Vaginal Smears in the Rat

LONG AND EVANS (1)	YOUNG, BOLING, AND BLANDAU (42)
STAGE I Small, round, nucleated cells only. Duration about 12 hours PROESTRUM	STAGE I From small, round, nucleated cells only, to 75 per cent cornified cells. Beginning of heat is when 25 per cent of the cells are cornified. Duration 8–11 hours
STAGE II Cornified cells only. Mating mostly in this stage ESTRUS	STAGE II From cornified cells only with ovulation early in this stage, to cornified 25 per cent, pavement nucleated cells 75 per cent
STAGE III Late cornified stage, abundant cheesy smear. Mating no longer allowed as a rule. Stages II and III last about 27 hours	STAGE III Pavement epithelial cells only
STAGE IV Cornified cells and leucocytes. Duration about 6 hours METESTRUM	STAGE IV Pavement cells and leucocytes
STAGE V Epithelial cells and leucocytes. Duration about 57 hours DIESTRUM	

always slender, with a slitlike lumen. It is lined by a simple columnar epithelium, and the glands are scanty. During vaginal stage I, or proestrum, there are marked vascular engorgement and an accumulation of fluid in the lumen, which distends to 5 mm. in diameter, in contrast to the diestrous diameter of 1.6 to 2.5 mm. The distension converts the columnar epithelium into a cuboidal one. Leucocytes are usually absent from the epithelium. These changes are continued in the early part of stage II, but at about the end of this stage the distension disappears, and the fluid is lost by drainage through the cervices. With the reduction in distension the uterine wall becomes flaccid, and the epithelium reverts to the columnar type, but the cells show signs of vacuolar "degeneration." During stage III the vacuolization increases, but regeneration is apparent in stages IV and V (1). Degenerated ova from the previous heat remain in the uterus and are washed out with the fluid in the uterus during heat (43).

During pseudopregnancy—a period in which the vagina remains in stage V—the main change is that more mitotic activity is found in the uterine epithelium at about 7 to 8 days after heat; the stroma also shows growth which precedes that of the epithelium by a day or two. The glandular changes at any time are but slight (44).

During the normal cycle the endometrium does not produce deciduomata after traumatization, but they may be produced in pseudopregnancy from the fourth to the seventh day (1,44). This reaction is due to the secretion of progesterone by the corpora lutea and affords evidence that this does not occur, either at all or as much, in the normal cycle as in the long cycle. On the other hand, during lactation, when the corpora lutea become active and persist, the endometrium remains sensitized from the fourth to the seventeenth day from delivery. After this time it is no longer sensitive (1,45).

OVIDUCT. The distal folds of the oviduct are distended by fluid at the time of ovulation, and during the 12 hours that the distension lasts the eggs are in this part of the tube (1). When the eggs are shed, they are surrounded by granulosa cells which are dispersed by the first spermatozoa to reach them. The average size of the eggs is $71 \times 76\ \mu$ (46). The tubo-uterine junction is 0.3 mm. from the tip of the uterus on the anterior side, not on the mesenteric side as in most mammals. The mucosal margin is slightly raised, and the last part of the tube is surrounded by a strong muscle (47).

PITUITARY. The cells of the anterior pituitary in relation to the cycle have been studied thoroughly, and the work has been summarized in a paper which also contains many original observations. It was found that the eosinophil cells do not vary in relative numbers during the normal cycle, but the granules are more distinct when the females are in heat. There is, however, a drop in the proportion of these cells during the lutein phases of pseudopregnancy and pregnancy. The basophilic cells become degranulated during diestrum (48).

Changes in the adrenal cortex in relation to the cycle have been described. The cells of the zona fascicularis and of the cell nests near the medulla are enlarged during heat, and their lipid content increases (49). Castration or ovariectomy of immature rats causes the gland to hypertrophy; if the operation is performed after puberty, however, atrophy results in females but not in males (50).

PHYSIOLOGY OF THE FEMALE TRACT

The application of X-rays to the ovaries of the immature rat in doses of 540 r produces precocious puberty, while 830 r, or more, produce castrate atrophy of the accessory organs (51). In the adult female the castration dose is approximately 3,000 r, but the corpus luteum is entirely resistant to radiation (52), and in some cases the rats still experience estrous cycles (53).

In general, the thyroid gland has little relationship to reproduction, but it has been reported that the feeding of 0.25 to 0.3 g. of thyroid substance daily to females for 3 to 5 days in the cooler parts of the year considerably increases the litter size. If it is done during hot weather, or if the dose is increased, adverse effects result (54).

It is well known that the thymus gland retrogresses at the time of puberty, but not in the gonadectomized animal. The injection of pituitary extract or of estrogens accelerates, or brings about, this change (55).

Pseudopregnancy is induced by the sensitization of the corpora lutea of the cycle when the cervix uteri is stimulated. It has already been mentioned that the reaction depends upon the integrity of the abdominal sympathetic chain. If the stimulation of the cervix is done by a single electric shock during late proestrum or estrus, 86 per cent become pseudopregnant at once. On the first day of diestrum 54 per cent react at once, and 34 per cent have one more cycle. On the second day 13 per cent react at once, and 54 per cent have one more cycle. Stimulation during pseudopregnancy does not prolong this period (56). Anesthesia of the animal during heat reduces the response considerably (57). Pseudopregnancy is also evoked by injecting prolactin; hence stimulation of the cervix is believed to cause the release of this hormone, which activates and maintains the corpus luteum (58).

The pH of the vaginal contents during the normal cycle is as follows:

Beginning of proestrum	pH 5.4
During estrus	pH 4.2
In diestrum	pH 6.1

In the ovariectomized rat the pH is 7.0, and, if 8 I.U. of estrogen are injected, it falls to 4.1 (59). These reactions are more acid than those recorded for most species.

In diestrum the amount of fluid in the uterus weighs 0.025 g., but in estrus 0.5 g. is present. Removal of the fluid greatly delays the passage of

spermatozoa through the tract (60). The pH varies with the stage of heat. The following figures may be quoted (61):

Stage I	pH 7.29
Stage II	pH 7.31
Stage III	pH 7.69
Stage IV (diestrum)	pH 7.43

It has been mentioned that ovariectomy does not always interrupt pregnancy if it is done during the last third of that period. If the embryos are removed, the placentae are retained for the normal time, and paraffin pellets also remain in the uterus if placentae are present, either in the same or the opposite uterus (62). If all fetuses but one are removed, pregnancy is continued when the ovaries are removed provided that the placentae are left *in situ,* but the birth mechanism is impaired. It would seem that part of the corpus luteum function is taken over by the placenta (63). This seems logical when it is remembered that the mare is normally able to go through most of pregnancy without corpora lutea.

The mean contraction rate of excised uterine muscle is lower (31 per hour) in estrus than in diestrum (52 per hour) (64) according to one paper, but according to another the reverse relationship holds. Contractions tend to begin at the tubal end (65). Anaerobic glycolysis and O_2 consumption are greatest at proestrum and lowest at the end of heat, but aerobic glycolysis shows the opposite relationship (66). Adrenalin inhibits contractions in all stages. The minimal effective dose *in situ* is 0.0005 mg. per kg. of body weight (67).

If the ovarian bursa is opened, fecundity is reduced (68). Probably this is due to the chance given the eggs to escape, as it will be recalled that the upper third of the oviduct is distended with fluid at the time when the eggs have been shed (1).

In the female rat creatine is absent from the urine only during diestrum; it is also absent if the rats are ovariectomized, and it reappears if estrogens are injected. It is absent in the mature male and present in the castrate, it is increased in amount following the injection of estrogens, and it disappears if androgens are injected (69). These results have been questioned (70). Choline esterase is higher in mature females than in young ones or in males. It falls after ovariectomy and is not restored by estrogens, but estrogen and progesterone together cause it to rise to normal, or higher (71).

There is a small quantity of estrogen in pregnancy urine but not in the placentae (72).

The pituitary of the rat is relatively rich in gonadotrophic hormones, and particularly so in follicle-stimulating hormone (73). The amount of gonadotrophic hormones present is high at birth, rises to the twenty-first day, then falls a little until puberty, when the fall becomes abrupt. The amount remains at a low level until old age, when it rises slowly. Up to puberty the content of the female pituitary is greater than that of the male, but afterwards their relative amounts are reversed; this is due not only to the fall in the content in the female but to a rise in that of the male (74,75,76). Ovariectomy causes the pituitary to become about 20 per cent more potent; it increases rapidly for the first 6 weeks after the operation, then the rate of increase becomes slower (77,78). The increase is mainly in F.S.H. content, and slightly in L.H. Injection of estrogen into the ovariectomized female lowers the L.H. content to below normal level and causes the F.S.H. to fall to just above the normal content (79).

The prolactin content of the pituitary of the female is about 0.28 bird units per mg. in the immature animal. It rises to 0.48 B.U. after maturity. During pregnancy it falls slightly, but in lactation there is a marked rise. After ovariectomy it falls gradually, reaching 0.18 B.U., which is practically the level in the normal male. The injection of estrogens or of progesterone raises the level to about 0.7 B.U. Treatment with 200 I.U. of estrogen daily for 20 days is more effective than higher doses, which tend to depress the prolactin content (80). Prolactin is responsible for the exhibition of maternal behavior, i.e., the retrieving and nursing instincts (81).

The level of estrogens necessary to induce the fully cornified vaginal smear has been accepted as the "Rat Unit" of estrogenic activity. Tests must be made under standard conditions on at least 20 mature ovariectomized females. The International Unit (I.U.) is approximately one third of the R.U. and is defined by the League of Nations Commission on Biological Standardization as the specific estrus-producing activity contained in 0.1 γ ($=$0.0001 mg.) of a standard preparation of estrone (82). The potencies of various steroid hormones have been determined in terms of Rat Units and are on record (83).

The properties of estrogen in causing vaginal and uterine changes and also copulatory responses can be demonstrated in the immature rat. The latter is relatively insensitive until 30 days after birth, when the effective amounts are 10 R.U. of estrogen followed by 0.4 mg. of progesterone in a

single injection (84), or 2 R.U. of estrogen daily for 3 to 4 days (85). Some differences in the response to various estrogens have been observed; estrone is more potent in causing cornification and uterine hypertrophy, and estriol is more potent in opening the vaginal introitus (86,87).

In mature ovariectomized rats threshold doses of estrogen do not produce continuous heat even when they are injected daily. After the normal length of estrus the females cease to be in heat. With daily doses of 3.75 to 10.0 I.U. (1 to 3 R.U.) a cyclical rhythm can be set up in many rats with a cycle length of $4.8 \pm .1$ days. If the pituitary, also, is removed, the mean length is the same, but with the additional removal of the adrenals cycles are suppressed, either anestrum or continuous heat ensuing. The cycles may be renewed in some cases if cortin is injected (88). Desoxycorticosterone and progesterone have the same effect (89).

Sexual receptivity is produced more effectively by the injection of progesterone along with estrogen than by estrogen alone. Thus, while 20 R.U. of estrogen alone produced receptivity in only 10 per cent of ovariectomized females and 100 R.U. in 90 per cent, 10 R.U. of estrogen with 0.4 I.U. of progesterone was 100 per cent effective (90).

Continued injections of estrogens into normal females are injurious to the ovaries; daily injections of 0.25 to 2.0 R.U. produce a state of continuous anestrum or of continuous heat. This is believed to be due to an effect of the estrogens upon the pituitary gland (91).

The injection of estrogens into the immature rat causes hypertrophy of the uterus. The maximal increase is brought about by 0.5 γ estradiol (6 R.U.), 0.075 γ increases the weight about 50 per cent, and 0.025 γ (0.3 R.U.) is without effect (92).

It is now believed that estrogens cause the persistence of the corpus luteum. In the rat a minimum of 50 I.U. estrogens daily is needed to produce this effect, but the corpora lutea so produced do not last beyond 20 days, their normal duration in pregnancy (93).

The level of progesterone needed to maintain pregnancy in the ovariectomized rat is about 2 Rab.U. daily; 1 Rab.U. daily maintained 3 pregnancies in 8; below 1 unit the injections were ineffective (94). This hormone, if injected into the normal pregnant rat, prolongs gestation for from 30 to 150 hours, but after 70 hours the fetuses are nonviable (95). In pseudopregnant rats after ovariectomy 1.5 Rab.U. given over 4 to 8 days were not sufficient to maintain the decidual reaction, but 3.0 Rab.U. and above were effective. Estrogen inhibits this effect if it is given in fairly large amounts,

but it augments the reaction in small doses. Thus, 0.15 γ of estradiol augments 1.5 Rab.U. of progesterone, but 3 γ inhibits the effect of 3 Rab.U., and 9 γ inhibits 6 Rab.U. but 0.6 γ augments them (96). Progesterone will not prolong the life of deciduomata indefinitely (97).

A very large amount of work, in which the rat has been used as the experimental animal, has been done upon the effects of gonadotrophic hormones and especially upon pituitary-gonadic relationships. As the object of this book is to bring together as far as possible the major quantitative data, much has been neglected unless it seemed to throw light upon the physiology of the species. We now give some data relating to the major reactions produced by these hormones.

The ovary of the immature rat will not respond to the injection of gonadotrophic hormones by the growth of follicles before 21 days, and apparently a well-developed granulosa is necessary for this to occur (98). F.S.H. alone will not cause the ovaries to develop beyond a weight of 45 mg., and L.H. alone will not cause any increase at all; but, if F.S.H. is present to cause follicular development, L.H. is able to act and will produce a large increase in weight (99). International and Rat standards have been adopted in some cases. These are measured by the amount of substance needed to double the weight of immature ovaries under certain standard conditions. At present there is some confusion as the method of testing varies with the laboratory. One of the most pressing needs is the adoption of standard methods of assay and their general application.

It is possible to obtain superovulation in immature rats by carefully regulating the dose, and in these animals as many as 23 young may be born, and up to 33 embryos have been found. The maximum prolificacy has been obtained when the rats were treated just before the normal time of puberty (100). Sixteen R.U. of P.M.S. is about the optimum dose for this purpose; a greater amount causes too much luteinization (101). With F.S.H. an average of 17 implantation sites was produced against a normal of 10 for mature rats. Ten to fifteen R.U. was the optimum dose, and the number of young born was almost never in excess of normal, and the average was 6.4 against 9.0 for normals (102). These rats were slightly younger than those used in the P.M.S. work. In mature rats superovulation is not produced, but the injection of 12 R.U. of P.M.S. in metestrum does increase the average litter size if the rats are bred at the next heat period, but not beyond the normal extreme (103).

The injection of 2 R.U. of estrogen daily for 30 days or more impairs the gonadotrophic function of immature rats (104), and 10 R.U. daily for 5 days degranulates the pituitary basophils and, to a lesser extent, the eosinophils (105).

Castration and ovariectomy cause changes in the anterior pituitary. The most marked of these is the production of highly vacuolated (signet-ring) basophil cells. These changes may be prevented in the female by a minimum of 2 B.U. of androgens daily, but the male requires 10 B.U. (106). Estrogens prevented changes when given daily in doses of 0.03 R.U. to females and of 0.4 R.U. to males (107). Progesterone does not prevent them in doses up to 3 mg. (108). Ovariectomy increases the gonadotrophic potency of the anterior pituitary. After 5 days the latter is nearly 4 times as potent as the normal; at 60 days, 31 times; and eventually, 52 times (109). These figures relate to the gland as a whole.

The minimum doses of hormones which will produce pseudopregnancy appear to be as follows: estrogen, 200 I.U. daily (110); testosterone, 2.5 to 5.0 mg. given over 10 days (111); testosterone propionate, 0.1 mg. daily for 16 days (112); progesterone, 1 mg. daily for 9 to 11 days (113). They act by modifying the anterior pituitary function.

Large acidophilic cells appear in the anterior pituitary during pregnancy. These cells increase in numbers from 3 days to 12 days, after which there is no further increase, but they persist throughout pregnancy and lactation. They also appear in pseudopregnancy and last about 12 days (114). Hypophysectomy before the eleventh day of pregnancy is followed by resorption of the fetuses; when performed at from 11 to 20 days of pregnancy, normal young are born after a prolonged gestation; but if the operation is performed on the twenty-first day, normal parturition follows (115). Pregnant mare's serum will not maintain pregnancy in early hypophysectomized rats, but 20 I.U. daily of prolactin does so in most cases (116).

Large doses of estrogens injected before the nineteenth day of pregnancy cause the death of the fetuses, but not after this time (117). Injection of 500 γ of testosterone propionate daily during late pregnancy delays parturition. If injected early it prevents, or modifies, fetal development (118). Injections made before the sixteenth day produce modifications in the accessory sex organs of female fetuses. Administration of 750 to 3,300 I.U. causes vasa deferentia to be produced in all female young, but intermediate doses above 300 I.U. cause them to appear in some of the fetuses. Androsterone is just as

effective on an I.U. basis, whereas androstene-dione is not quite so effective. The order of sensitivity of the tract in increasing difficulty of modification is as follows:

Ventral prostate
Posterior prostate
Coagulating gland
Seminal vesicles
Vas deferens and epididymis

The Wolffian duct of the left side is more sensitive than that of the right (119). Similar injections of estrogens produce effects in male embryos. With injections of 1.0 mg. of estradiol dipropionate slight hypospadias was produced in male fetuses; with 2.0 mg. there was a change in the position of the gonad and the degree of hypospadias increased, or the external genitalia were modified toward the female. From 3.0 mg. upwards the injections caused the external genitalia to be female. No effects were observed upon the testes, but there was a relative inhibition of the epididymis, vas deferens, and prostate. The Mullerian ducts remained vestigial (120).

A summary of the relationships between body weight and the weights of parts of the reproductive tract, together with much data on prenatal growth, has been published in convenient form (121).

THE MALE

In male rats in the University of Chicago Colony sperm heads appear in the testes at 33 to 35 days of age. Treatment with anterior pituitary preparations did not hasten their appearance by as much as 2 to 3 days, but it did accelerate the development of the accessory tract (122).

The plug formed in the vagina during copulation has two prongs which fit into the cervices. The vulval end is pointed in contrast to that of the mouse, in which species it is blunt. It gradually disappears by disintegration (123). The semen is, in part, injected directly into the uteri, as spermatozoa appear at the apices within 2 minutes after copulation (124). By 15 minutes after coitus they are in the uterine segment of the oviduct in 42 per cent of cases, and in the ovarian segment in 21 per cent. In 30 minutes the corresponding figures are 88 and 62 per cent. After an hour has elapsed spermatozoa can be found throughout the tract in all cases. Only a small proportion of those which are deposited in the female reach the infundibulum (125).

The copulation plug appears to be necessary for the effective insemination

of the female, in spite of the belief that some semen is injected directly into the uterus. Removal of the vesiculae seminales and the coagulating gland, a portion of the prostate, was followed by infertility in the majority of instances. In some cases where the operation was apparently incomplete, spermatozoa were found in the uteri only when a plug had been formed (126).

Spermatozoa can survive in the uterus up to 12 hours, in the vagina for 14½ hours, and in the oviducts for 16 to 17 hours (127). Those which are stored in the epididymis, with the vasa efferentia ligated, remain capable of motility for 42 days, and of fertility for 21 days (128). If the testes are anchored in the body cavity, sperm survival is not affected, but castration reduces their life to 14 days (129). Testes which are anchored in the abdominal cavity cease sperm production within 5 days, but there is no diminution in the output of hormones, at least up to 60 days (130).

The pH of various parts of the male tract has been given as follows (131):

Testes	pH 7.2 –7.4
Epididymis	pH 6.5 –6.6
Prostate	pH 7.14
Seminal vesicles	pH 6.32–6.34

The effects of the failure to produce testosterone after castration are made apparent by a degranulation of seminal vesicle cells in 2 to 3 days (132), and by similar damage to the prostate cells within 5 days (133). The weight of the seminal vesicles decreases to about one fifth in 5 weeks, but subsequently a partial recovery ensues (134). This may possibly be related to the secretion of androgens by the adrenal cortex, as this organ is able partially to maintain the weight of the ventral prostate in the castrated rat; the effect, however, is said to cease after they are 31 days old (135). The vas deferens does not have spontaneous motility but acquires it after castration (136). Androgens restore the immotility, but estrogens do not (137).

The ventrocaudal part of the scrotal sac is reddish yellow in color and is wrinkled. These are secondary sexual characters as they are lost after castration (138). After this operation the scrotum loses weight and its muscle contracts with much less readiness than formerly (134).

In the Long-Evans strain the prepuce begins to cornify at 31 days of age, cleavage to two surfaces begins at 45 days, and separation is complete at 52 days. If the rats are castrated at 26 days of age, 0.012 mg. of testosterone propionate daily causes separation in 3 weeks, and larger doses shorten the time (139). If rats are castrated at birth, the minimal effective daily dose of

testosterone needed to grow the accessory organs is: to 20 days, 0.03 mg.; at 30 days, 0.025 mg.; and from 40 to 60 days, 0.005 mg. After this time the amount needed increases rapidly to 0.025 mg. (140). In adult life the amounts needed daily to maintain various structures are given below:

	PROSTATE	SEMINAL VESICLES WEIGHT	SEMINAL VESICLES GRANULES
Androsterone (141)	1 mg.	$>$ 2 mg.	
Testosterone (142)	0.03–0.05 mg.	0.2 mg.	0.6 –0.7 mg.
Testosterone propionate (142)		$<$ .05 mg.	0.15 mg.

The amount of testis tissue needed to maintain normal prostate and seminal vesicles is 0.07 g., or 3.1 per cent of the total testis weight (143). It may be inferred that the testes are capable of secreting about 20 mg. of testosterone daily if the fragment of testis continues to secrete at the normal rate, an ample margin of safety.

In the immature rat the daily injection of .05 mg. of testosterone propionate prevents normal testicular growth (144), but higher doses, i.e., 30 mg. a week for 4 weeks, stimulate the growth,—unless they are continued for a longer period, when inhibition results (145). In immature hypophysectomized rats 2 mg. daily induces sperm formation. Smaller doses are ineffective though they stimulate growth of the accessory organs (146).

The anterior pituitary of the castrate is twice as potent in gonadotrophic hormone as is that of the normal (77). The potency is mainly in F.S.H., and it continues so to the twentieth day; from then to 9 months more L.H. is produced, and after that time F.S.H. again (147).

The injection of 1 R.U. of P.M.S. daily in immature rats caused the testis tubules to develop, but no hastening of spermatogenesis was observed. The interstitial tissue also developed. High doses caused tubule damage (148). The daily injection of 0.5 M.U. of P.M.S. maintained the testis weights of hypophysectomized rats if the injections were started at once, but did not maintain fertility; 1.0 M.U. daily was necessary to do this. If treatment was delayed, 5 M.U. were needed to maintain testis weights, but fertility was lost. Pregnancy urine was less effective in immediate treatment, but more so in delayed treatment (149). The daily injection of 10 to 25 R.U. of pregnancy urine into normal immature rats did not hasten puberty, but, injected into immature hypophysectomized rats, it caused development of the interstitial tissue and accessory organs, though regression set in after about 30 days (150).

The prolactin content of the pituitary of the male is about 0.16 B.U. per mg. of tissue. It varies little in the cryptorchid, but falls to about 60 per cent in the castrate (80).

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Other MURIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Acomys cahirinus Desmarest Cairo Spiny Mouse			11½ days	Egypt
A. ignitus Dollman	Jan.–Oct. (Heller)	1–2		E. Africa
A. percivali Dollman	July–Oct. (Heller)	1–2		E. Africa
A. wilsoni Thomas	Embryos July (Heller)	1, 4		E. Africa. 2 records
Aethomys chrysophilus De Winton African Bush Rat	Embryos Oct.–Nov. (Shortridge)	2–4		Cent. and S. Africa
A. namaquensis A. Smith South African Rock Rat	Breeds all year (Shortridge)	2–5		S. Africa
Apodemus fodiens Schreber			21 days	N. Europe and Asia
A. sylvaticus L.	Probably polyestrous (Heape). Most of year. Cycle 6 days; post-parturient heat (Laver)	2–9, usually 4–5; mean $4.8 \pm .1$	23–26 days	Europe and W. Asia
Cricetomys gambianus Waterhouse Giant Rat			42 days	N. and Cent. Africa
Dasymys helukus Heller Shaggy-haired Rat	Embryos Jan., Aug. (Heller, Loring)	3		E. Africa. 2 records
D. nudipes Peters Water Rat	Apr.–Oct. (Hill, Shortridge)	2–4		Angola

Other MURIDAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Leggada bella Thomas Pygmy Mouse	Embryos Aug. (Shortridge)	3–5		E. and Cent. Africa
Lemniscomys griselda Thomas Single-striped Grass Mouse	Polyestrous (Fitzsimons)	5–12 (Fitzsimons); 2–4 (Hill)		E. and S. Africa
L. striatus L. Striped Grass Mouse	Oct.–Dec. (Sanderson)			E. and W. Africa
Malacomys longipes Milne-Edwards	March–June (Sanderson)			Cent. Africa
Micromys minutus Pallas Little Harvest Mouse	Probably polyestrous (Heape). In summer (Laver)	5–9, usually 6–8	21 days	Europe and Asia
Millardia meltada Gray Metad Rat		6–8		India
Nesokia kok Gray Indian Mole Rat		8–10		India
Notomys gouldii Gray		4–6		Western Australia
Ochromys woosnami Schwann Desert Rat	Embryos Nov. (Shortridge)	2		S. Africa. 1 record
Oenomys hypoxanthus Pucheran Rufous-nosed Rat	Oct.–Apr. (Sanderson)			E. and W. Africa
Pelomys frater Thomas Creek Rat	Born about Apr. (Hill)	2–3		Angola

Other MURIDAE (*Continued*)

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Rhabdomys pumilio Sparrman Striped Rat	Polyestrous, Sept.–Apr. (Fitzsimons)	3–8		E. and S. Africa. Puberty at 3 mos. (Powell)
Thallomys damarensis De Winton Damara Tree Rat	Embryos Sept., Oct. (Shortridge)	1–4		S.W. Africa. 2 records
T. nigricauda Thomas Black-tailed Tree Rat	Sept.–Apr. (Shortridge)	2–4		S. Africa
Vandeleuria oleracea Bennett Long-tailed Tree Mouse		3–4		India

APLODONTIIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	HABITAT, ETC.
Aplodontia rufa Rafinesque Mountain Beaver	Born mid-Apr. (N.A.F. 55)	2–3 or 5–6	Western N. America

ZAPOTIDAE

Zapushudsonius Zimmermann

JUMPING MOUSE

The jumping mouse of central and eastern North America has one litter a year in New York (1), and probably in North Dakota (2), but further

south it has more, sometimes in July or, more frequently, in September. In the north the season of mating is May, and the young are born in June (1). The litter size is 5 to 8, mean 7.0.

1. Hamilton, W. J., Jr. Am. Midland Nat., 16: 187–200, 1935.
2. Bailey, V. North American Fauna, No. 49, 1926.

Other ZAPOTIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	HABITAT, ETC.
Napaeozapus insignis Miller Woodland Jumping Mouse	Born late June to early July, sometimes second litter Sept. (Hamilton)	3–6, usually 4	Eastern N. America
Zapus princeps Allen		4–7	Rocky Mountains
Z. trinotatus Rhoads	One litter a year (N.A.F. 55)	4–8	Western N. America

JACULIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Dipus sagitta Pallas Jerboa	Apr.–Aug., mostly mid-May to mid-Aug. 2 litters a year	2–5; mode 3, mean 3.0 ± .05		E. Europe, W. Asia. Early young breed year of birth (Fenink and Kazantzeva)
Jaculus orientalis Erxleben Jerboa			42 days	N. Africa

BATHYERGIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	HABITAT, ETC.
Cryptomys damarensis Ogilby S.W. African Mole Rat	Born Apr. Probably a fixed breeding season (Shortridge)	5	Testes in body
C. mechowii Peters Large Mole Rat	Born Jan.–Feb. (Hill)	1–2	Angola. Has an osclitoridis (Thomas)

THRYONOMYIDAE

Thryonomys swindlerianus Temminck Cane Rat	Born June–Aug., probably fixed breeding season (Shortridge)	2–4, usually 3	W. Africa

CTENODACTYLIDAE

Ctenodactylus gundi Rothmann Gundi	Two breeding seasons, Jan. and Apr. Birth March and June	1–2	N. Africa
Petromus typicus A. Smith Dassie Rat	Sept.–Feb. (Shortridge)	1–2	S. Africa

PEDETIDAE

Pedetes cafer Pallas Spring Hare	Breed once a year, Apr. (Shortridge)	1, twins very rare	S. Africa
P. surdaster Thomas		1 always	Cent. Africa

ERITHIZONTIDAE

Erithizon dorsatum L.

PORCUPINE

The common porcupine of North America mates during November. At this time the hair surrounding the mammary glands of the female temporarily acquires a cinnamon coloration. The number of young is nearly always 1; twins are very occasional. The period of gestation is 16 weeks (1).

1. Struthers, P. H. J. Mammalogy, 9: 301–308, 1928.

Erithizon epixanthum Brandt

YELLOW-HAIRED PORCUPINE

The yellow-haired porcupine which inhabits western North America has a breeding season in September and October (1). The number of young is usually 1, but 2 are occasionally born. The duration of gestation has been given as 9 months, a length which must be queried in view of the known length in *E. dorsatum*.

1. Bailey, V. North American Fauna, No. 55, 1936.

HYSTRICIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Hystrix africae-australis Peters South African Porcupine	Two litters a year (Haagner)	1–4, usually 2	6–8 weeks	S. Africa
H. cristata L. European Porcupine			63 days, 112 days	
H. hodgsoni Gray Crestless Himalayan Porcupine	Spring (Blanford)	2		India
H. leucura Sykes Indian Porcupine		2–4		India

ECHIMYIDAE

Proechimys semispinosus True		2–3		Cent. America

DASYPROCTIDAE

Dasyprocta agouti L. Agouti			104 days	S. America
D. punctata True Agouti	No fixed season (Enders)	2–4, usually 2		Cent. and S. America. Bursa incompletely surrounds the ovary

CAVIIDAE

Cavia porcellus L.

GUINEA PIG

The guinea pig in the laboratory is polyestrous all the year round. Heat lasts for less than half a day, and the complete cycle is 16½ days. The cyclical changes in the female tract of the guinea pig have been studied in more detail than in any other mammal. The vaginal smear is a clear indication of the reproductive state, and its detailed investigation made possible the recent rapid developments in the fields of hormone isolation and physiological analysis. The number of young is usually 3 to 4, and the duration of gestation is about 67 to 68 days, a very long period for so small an animal. Ovulation is spontaneous and the corpus luteum of the cycle is functional, in contrast to the condition found in all the Muridae which have been investigated. The vagina is closed by a membrane, which opens spontaneously at heat and which thus provides a useful index of heat if it is read in conjunction with the vaginal smear.

THE ESTROUS CYCLE

The age of puberty in the guinea pig is from 55 to 70 days under normal conditions of management. If the food is richer than usual, causing more rapid growth, puberty may occur at from 45 to 60 days; slow growth on poor food delays its onset. Puberty occurs at the same time whether males are kept with the females or not (1). One series of records gave a mean age at first heat of 67.8 ± 2.0 days, with a standard deviation of 21.5 days, and a spread from 33 to 134 days. In this work it was found that the mean age at first rupture of the vaginal closure membrane was 58.2 days. The usual interval between first rupture and heat was from 0 to 4 days, and an appreciable number of the long intervals were the duration of a cycle or a multiple of it, suggesting that in some cases the earlier heats are not so intense as later ones (2).

The duration of the estrous cycle is usually given as 16½ days. One set of data gives a modal length of 16 days (3); another, 17 days with a mean of 17.7 ± 1.8 days (4); and another a modal length of 15 to 16 days with a mean of 16.34 ± .10 days, standard deviation of 1.89 days, and a spread of

13 to 25 days (5). A series in which the animals were observed at two-hour intervals instead of daily or twice daily gave a mean cycle length of 16 days, 6 hours. As heat begins most frequently in the evening, the distribution shows a double mode, at 16 and 17 days (6). Vasectomized copulation does not modify the cycle length (7,6).

Proestrum, in which there is congestion and swelling of the external genitals and a slight serous discharge from the vagina, usually lasts from 1 to 1½ days, and heat or sexual receptivity lasts 6 to 11 hours in 90 per cent of all cases (1). Another investigation gave an average of 8.21 ± .07 hours, with a range from 1 to 18 hours, for the duration of heat (6). The vagina usually remains open about 4 days (4). Ovulation occurs usually at 10 hours after the beginning of heat or sexual receptivity. There is no relation between the length of heat and the number of follicles which rupture (8), but the number is highest in those females with the most intense heat, as judged by the frequency with which they are mounted (9). About 64 per cent of all heat periods begin between 6 P.M. and 6 A.M., but during the months of short daylight, i.e., October to December, the curve of distribution of the onset of heat shifts about 2 hours and heat tends to begin earlier in the afternoon (6). If the females are kept in the dark, they come in heat at any time; the tendency for heat to begin in the evening vanishes. Guinea pigs so kept do not change the length of the cycles nor the duration of heat (10).

There is little or no difference in the number of ovulations from the two ovaries, since 51 per cent of embryos were found in the left horn of the uterus (11). As internal migration of ova is held to be impossible on anatomical grounds (12), this must represent the proportion of ova shed from the ovary. The absence of internal migration has also been shown experimentally (13).

The removal of corpora lutea immediately after heat shortens the cycle to 11 days (14). This represents an exceptionally long time required for the ripening of new graafian follicles. Heat occurs immediately after parturition in about 64 per cent of females. It usually begins within 2 hours of the end of parturition but is short, lasting 3.5 hours instead of the normal average of 8.6 hours. It is always associated with ovulation, though more than half of those guinea pigs which did not come in heat had ovulated (15).

Insemination at different times has given a maximum life for the ovum of 30 hours, but within about 8 hours after ovulation the number of normal pregnancies and of eggs fertilized drops markedly. The data are summarized below (16):

TIME OF INSEMINATION	PER CENT PREGNANT	AVERAGE LITTER SIZE	PERCENTAGE OF NORMAL PREGNANCIES
HOURS AFTER OVULATION			
Controls	83	2.6	88
8	67	1.7	66
14	56	1.6	27
20	31	1.3	10
26	7	0	0
32	0	0	0

Pregnancy is said to be rare following a copulation in the first 3 or 4 hours of heat (1). The eggs arrive in the uterus about 3½ days after they are shed (17).

The average litter size for a very large number of individuals was 2.58 ± .006; the range was from 1 to 8; the standard deviation, 1.02; and the mode, 2 to 3. It is highest in spring and summer (18). The mode of the duration of gestation is 68 days, with a distribution of 58 to 72 days (16). Parturition occurs equally at any time of day (15).

The sex ratio is 50.59 ± .19 males. Variations with litter size are not significant (18). The sex ratio of fetuses of various ages is 55.9 ± 2.09 (11).

HISTOLOGY OF THE FEMALE TRACT

OVARY. The cavity in some graafian follicles is established when the guinea pig is 4 to 7 days old, but the theca interna is not well differentiated at this time; mitoses are frequent throughout the ovary. At 18 days atresia has begun in many follicles (19). There is a wave of follicular growth during the cycle which begins 2 to 3 days after ovulation. The follicles grow at a constant rate until the beginning of heat, when rapid development sets in. Those which will rupture protrude from the surface of the follicle; the tunica albuginea is reduced so that the germinal epithelium and a much-thinned granulosa layer alone cover the follicle at the rupture point (20). The ovary of the guinea pig is remarkable for the extent and variety of forms of follicular atresia. The wave of follicular growth before heat produces in each ovary about 40 to 50 follicles with cavities, of which only about 2 are destined to rupture. Those which will not rupture can be detected about 2 days before heat by degenerative changes in the granulosa next the theca interna. The nucleus of the ovum in these follicles is active, and the chromo-

somes arrange themselves along the equator of the spindle, where they remain. In a follicle which will rupture they are able to separate, and the first polar body is produced before ovulation. In the degenerating follicles the granulosa cells break up and are usually removed by cytolysis, but occasionally by phagocytosis, leaving a cavity which is reduced by the proliferation of the theca interna. In the smaller of these follicles the theca interna proliferates rapidly and encloses the egg, which often fragments (7). This has been interpreted as a parthenogenic development (21,22) but, in the opinion of the writer and of others (23,24), the changes are definitely degenerative in nature. Unilateral ovariectomy doubles the number of ovulations from one ovary (9).

The ripe follicle is about 0.8 mm. in diameter, and the ovum measures about 65 μ. When the follicle ruptures there is little hemorrhage, but a small pool of follicular fluid is retained in the center of the developing corpus luteum for 2 to 3 days. The formation of the corpus luteum proceeds along classical lines, but the theca interna, perhaps, contributes to a greater degree than it does in other species. Fatty degeneration sets in at about the thirteenth day of the cycle, and the corpus luteum is reduced to a few strands of connective tissue cells, which gradually merge with the stroma of the ovary. The mature corpus luteum is oval in shape, at right angles to the surface of the ovary, and it is very difficult to extirpate completely because of its depth and the high vascularity of the ovarian stroma (25,7).

A striking feature of the ovary of the guinea pig is the great frequency with which cysts of the rete ovarii develop (9).

VAGINA. During diestrum the vaginal epithelium is thin, consisting at first of a low stratified squamous type with a ragged appearance. After 8 to 10 days it becomes more regular and the lower layer is cuboidal or columnar, with long flat cells overlying it. As heat approaches, an intense proliferation takes place; the epithelium becomes several cells thick, with the superficial layers flattened. At the beginning of heat these cells cornify and tend to desquamate, a process which becomes more rapid as heat continues. Toward the end of heat the vaginal wall, which has become very congested and edematous, is invaded by large numbers of leucocytes, which penetrate through the epithelial layer and pass into the lumen. Desquamation is particularly severe during metestrum, but repair soon sets in and the epithelium is restored to the typical diestrous state. During pregnancy the epithelium changes to a high columnar mucous type (26,27). The vaginal smear changes during heat and metestrum. At the beginning leucocytes disappear, squamous

epithelial cells are present, followed by cornified cells, then by small epithelial cells, and lastly by an invasion of leucocytes. A late stage of metestrum has been described (26) in which red blood cells are present; this has been denied by others (28), but in the writer's experience it occurs occasionally and is caused by bleeding from the uterus. An outline of the various schemes which have been suggested for classifying the stages of the cycle is given in table 4. The smears in the postparturient heart are not typical (27).

TABLE 4. Vaginal Smears of the Guinea Pig

STOCKARD AND PAPANICOLAOU (26)	SELLE (28)	YOUNG (29)
STAGE I a. Squamous epithelial cells staining gray with H. and E. Pycnotic nuclei; abundant mucus	STAGE I	STAGE Ia Superficial cells only, 25 per cent come in heat
b. Cornified cells staining red with H. and E.	STAGE II	STAGE Ib Early: less than 25 per cent cornified Middle: 25–75 per cent cornified } 60 per cent in heat Late: 75 per cent or more cornified. 15–20 per cent in heat Ovulation in Stage Ib
STAGE II Nucleated epithelial cells; smear abundant and cheesy	STAGE III Cornified and small epithelial cells, or epithelial cells only	STAGE II
STAGE III Liquefaction of cheesy mass; cells as last, with numerous leucocytes	STAGE IV	STAGE III
STAGE IV Slight hemorrhage, not always present	Absent	

UTERUS. During the vaginal stage Ia there is some growth of the uterine epithelium, the cells are tall and pseudostratified, and the surface tends to be irregular. The glands are not well developed, are inactive, and contain no mitoses. In stage Ib the mucous layer becomes very edematous, and the

usual leucocytic invasion begins. Rare mitoses may be found in the glands. In stage II the epithelial cells tend to become vacuolated. In stage III vacuolization increases, the epithelium breaks, patches are shed, and the leucocytic invasion is well marked. At 1 to 2 days postestrum the uterine wall is still somewhat broken, but edema has subsided and repair is in progress; a few mitoses are present in the gland cells but not in the stroma, which is very vascular. The glands are swollen with secretion. At 3 days the glands are much more tortuous, the cells are swollen so as to obliterate the lumen which has hitherto been open, and mitoses are abundant. The epithelium is tall, with nuclei at the bases of the cells, the upper margins of which are level. Mitosis has ceased. The mucous layer is thicker. At 7 days the gland cells have secreted into the lumen and hence have shrunk in size. The epithelium is cubical to columnar, and mitoses are common in the stroma cells. At 10 days the glands are retrogressing and are less coiled; at 14 days the retrogression is still more apparent. Occasionally in metestrum one finds extravasation of blood, which gathers as hematoma below the epithelium and passes into the lumen of the uterus, and hence into the vaginal smear. In one guinea pig seen by the writer the hemorrhage was so severe that it killed her (30, 7).

OVIDUCTS. The tubo-uterine junction is very complex. The isthmus is tortuous with moderately firm muscular wells. The mucosa has 4 major primary folds with a minor primary fold in the furrow between each pair. The tube passes through the uterine wall at right angles to the uterus and opens into the cavity about 0.5 mm. from its tip. The entrance is guarded by mucosal lips which are glandular. A thick spincterlike muscle extends into these lips. The tube is further guarded, just before its extension into the uterus, by a papilla which projects into its lumen (31). Attempts to force fluid from the uterus into the oviducts failed; the uterus always ruptured first (32).

PITUITARY. Variations in the number of cells of different types in the anterior pituitary in relation to the cycle are not statistically significant. Granulation is highest at 6 to 8 days postestrum, then falls, rises again to the beginning of heat, and falls rapidly during heat. These remarks apply both to acidophils and basophils. The Golgi apparatus hypertrophies during the first half of the cycle and tends to fragment during the second half. The mitochondria tend to concentrate in the Golgi zone while it is intact, and to scatter when it is not. They tend to concentrate at the periphery of many cells in proestrum and estrus (33). The degranulation during heat has been

observed by others (34). There are no special pregnancy cells, but both types of chromophils tend to degranulate at this time (35). The special type of castration cells formed after operation in many species is not found in the guinea pig of either sex (35,36).

It is said that the thyroid gland undergoes cyclical proliferation which is connected with the estrous cycle. It is at a maximum at 4 to 8 days after heat and at a minimum at 8 to 10 days (37).

PHYSIOLOGY OF THE FEMALE TRACT

The estrous cycle is upset if the uterus is removed. This is due to the persistence of the corpus luteum, which may last for a considerable time (38,39). Hysterectomy during heat or in gestation prevented the recurrence of cycles for at least 5 months. If the operation was performed before puberty, the first heat occurred at the normal time, but the corpora lutea persisted and no further heat periods ensued (40). This phenomenon is shown in a reduced degree by the rabbit but not by the rat. Its cause is obscure and requires further work.

Ovariectomy before the twenty-sixth day of pregnancy has always resulted in abortion or resorption of the embryos, but after this time, occasionally, the pregnancy continues normally (41,42).

If the uterine mucosa is traumatized at any time from the third to the eighth or ninth day after heat, deciduomata are produced. The reaction depends upon the presence of the corpora lutea (43), and it has been elicited in other species and in ovariectomized animals given progesterone.

Contractions of the uterus are not so great, but are more frequent, during diestrum when the corpora lutea are active (44,45). The frequency is highest at 4 days postestrum, and it slows to the rate found during heat by the tenth day. In the ovariectomized female the uterine muscle has the same slow rate of contraction, but the injection of 1 mg. of progesterone increases it beyond that found during the cycle, and 2 mg. still further increases the rate (45).

No estrogens have been found in the urine during diestrum, but when the female is in heat 250 R.U. per liter have been observed. During early pregnancy there is none; at 20 days, 250 R.U. per liter; and at 40 to 63 days, 500 R.U. per liter (46).

The gonadotrophe level of the pituitary is low, one quarter (or less) that of the rat; ovariectomy increases the amount whereas estrogens depress it (47).

Follicle stimulator is low, and it appears to be at its maximum just before heat (48). Luteinizer is at least ten times less than the level in the rat's pituitary (49).

The prolactin content of the pituitary is low; in immature females it is 220 B.U. per g., in mature females 520 B.U. per g. In lactating females and in males it is higher, and the injection of estrogens also raises it (50). The level is higher during heat than it is in diestrum (51).

It is very difficult to induce sexual receptivity in the spayed female by the injection of estrogens, but the injection of 40 I.U. of estrogen, followed 36 to 48 hours later by 0.2 I.U. of progesterone, invariably caused the females to be receptive to the male (52). In later experiments the use of 50 I.U. of progynon B (estradiol benzoate in oil) as the primer, with 0.1 I.U. of progesterone, was successful in 73 per cent of the animals. Lower doses were much less effective, but when the progesterone was increased to 0.4 I.U., the successes rose to 92 per cent. When the dose of progesterone was kept at 0.2 I.U. and the priming dose was varied, 20 I.U. of estrone was 33 per cent successful and the percentage rose gradually to 80 per cent with 50 I.U., after which there was not much gain (53). At 2 to 6 days of age the immature females are entirely unresponsive to these injections, but at 15 days there is some response, and a complete response is given at 30 days of age (54).

The spayed adult guinea pig requires 0.65 I.U. of progesterone daily for 6 days to sensitize the endometrium so that it will produce deciduomata. If the injections were preceded by estrogens, the reaction was slightly intensified. Continued progesterone injections caused the uterine mucosa to become refractory. Immature animals required 1 I.U. daily to produce sensitivity (55). In the normal animal a minimum of 100 to 160 R.U. of estrogen suppresses the power to give a decidual reaction (56).

The ovary of the guinea pig is very refractory to the injection of gonadotrophic hormones or to pituitary implants. This is largely due to the ease with which the theca interna of the follicles becomes luteinized. It is most difficult to grow normal follicles, but it can be done by the implantation of four guinea pig pituitaries daily (7).

The injection of P.M.S. into immature females causes little increase in ovarian weight, but the uterus is greatly enlarged (57). Injection into adults 3 to 5 days before heat was expected caused a great growth of the ovaries. These organs increased with progressive increase in dosage to 350 per cent at 150 R.U., and to 400 per cent with 500 R.U. The increase was mainly due

to theca luteinization and, at the higher doses, edema; but there was some granulosa luteinization, especially at the higher levels. The uterus increased in weight, with a maximum increase at 100 R.U., after which it became less with progressively higher doses. Heat occurred at the usual time, but ovulation was suppressed as there were no follicles in a condition to rupture (58). The injections caused an enlargement of the clitoris similar to that found when pregnancy urine is injected (59). The injection of 4 mg. of testosterone propionate daily prevents follicular growth and ovulation (60).

The relaxation of the pelvic girdle normally found at parturition and the need of the corpus luteum hormone, relaxin, to produce this effect have been investigated (61). The prenatal growth of the guinea pig has been the subject of considerable study (11,62).

THE MALE

The growth rates of the testes and accessory organs accelerate from 30 to 40 days of age. Electric ejaculation technics show that some secretion is present at 21 days at the earliest, and most males respond at 30 days. The first spermatozoa appear at 50 days, and their production is fairly uniform by 70 days (63). If one testis is removed before puberty, hypertrophy occurs in a few cases. This is believed to be not compensatory hypertrophy but an acceleration of growth (64).

Spermatozoa stored in the isolated epididymis retain their fertility for 20 to 35 days, and they remain motile for 59 days (65). If the epididymides are placed in the abdomen, motility lasts only 14 days. If they are scrotal but the testes are removed, motility ceases after 23 days (66). The injection of androgens increases both motility and survival time (67).

Electric ejaculation is a convenient means of obtaining semen for study. The male is lightly anesthetized. One electrode is placed through the skin on the back of the neck at the base of the skull. The other, a blunt one, is put in the mouth and a 33-volt A.C. current is passed. The normal amount of semen thus produced is 1.5 to 3 g. There is no seasonal difference in the amount (68).

Spermatozoa probably take 14 to 18 days to pass through the epididymis. If it is isolated from the testis, the time increases to 25 to 35 days (69). In the female they retain their fertility for 22 hours, but beyond 17 hours it is reduced (70).

A copulation plug is normally formed in the vagina after coitus. If the

proximal prostatic lobe is removed, this no longer happens. The anatomy and histology of the prostate is described in detail in this paper (71), and the seminal vesicles, which are large and produce a jellylike secretion, have also been carefully investigated (72).

The accessory organs tend to increase in weight up to 600 g. of body weight. Castration causes them to decrease to 50 per cent of their former weight, a reduction which is usually complete by 30 days after castration (73). Castration also leads in the young guinea pig to arrested atrophy and subsequent hypertrophy of the thymus (74).

After hypophysectomy the testes decrease from 2.5 to 3.5 g. (the normal weight) to 0.5 g. This decrease takes 45 days, but spermatogenesis ceases at 35 days. Spermatozoa are found in the tubules to 56 days, though they are few after between 5 and 14 days. The rate of decrease of the accessory organs is at about the same rate as after castration (75). After hypophysectomy the injection of 3 mg. of testosterone propionate daily preserves spermatogenesis in most of the tubules (76).

In the normal male 2 mg. daily of androgens for 30 days causes atrophy of the testes, but this effect is prevented if an extract of horse pituitary (rich in F.S.H.) is also given. There are differences in the responses of the prostate and seminal vesicles to individual androgens (77).

The pituitary of the male contains twice as much gonadotrophe as that of the female. In the cryptorchid and castrate the content rises about 70 per cent (47).

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The accessory organs tend to increase in weight up to 600 g. of body weight. Castration causes them to decrease to 50 per cent of their former weight, a reduction which is usually complete by 30 days after castration (73). Castration also leads in the young guinea pig to arrested atrophy and subsequent hypertrophy of the thymus (74).

After hypophysectomy the testes decrease from 2.5 to 3.5 g. (the normal weight) to 0.5 g. This decrease takes 45 days, but spermatogenesis ceases at 35 days. Spermatozoa are found in the tubules to 56 days, though they are few after between 5 and 14 days. The rate of decrease of the accessory organs is at about the same rate as after castration (75). After hypophysectomy the injection of 3 mg. of testosterone propionate daily preserves spermatogenesis in most of the tubules (76).

In the normal male 2 mg. daily of androgens for 30 days causes atrophy of the testes, but this effect is prevented if an extract of horse pituitary (rich in F.S.H.) is also given. There are differences in the responses of the prostate and seminal vesicles to individual androgens (77).

The pituitary of the male contains twice as much gonadotrophe as that of the female. In the cryptorchid and castrate the content rises about 70 per cent (47).

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CHINCHILLIDAE

Chinchilla laniger Bennett

CHINCHILLA

The chinchilla, a native of South America, breeds at any time of the year but is said to mate most readily in December and March (1), though according to one account most litters are born in September and January. Mating is nocturnal (2). A copulation plug is formed, which is shed entire, surrounded by the cornified layer of the vaginal wall. It hardens rapidly on exposure to the air. The estrous cycle is said by breeders to last 24 days and heat for 2 days (3). If it is correct, this is a surprisingly long cycle length, but it is similar to that of the nutria, which is rather closely related to the chinchilla. The period of gestation is 105 to 111 days (2), or 111 days, and 1

to 4 young are born at a time (4). The female experiences a postparturient heat 12 hours after she has given birth (5).

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Other CHINCHILLIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Chinchilla brevicaudata Waterhouse		1–2	125 days	S. America
Lagostomus tridactylus Brookes Viscacha	In England, any month of year; in Argentina, only in fall (Zuckerman). Late Apr. (Hudson)	2–3, usually 2	145 days	Southern S. America

CUNICULIDAE

Cuniculus paca True Spotted Cavy		1		Mexico and Cent. America. 1 record (Enders)

HYDROCHOERIDAE

Hydrochoerus hydrochoeris L. Capybara			119–126 days	S. America

CAPROMYIDAE

Myocastor coypus Molina

NUTRIA

The South American coypu is bred for its fur and is known commercially as the nutria. The females are polyestrous, though in order to get them to breed through the winter the temperature must be kept at 60° F. (1). The cycle in young animals is 24 to 27 days, rarely 14 to 17; in older ones it lasts 27 to 29 days. Heat lasts 2 to 4 days; it is rarely shown above the age of 3½ to 4 years (2). The shorter period quoted suggests that there may be pseudopregnancy in this species. The female first mates at the age of 8 months (1). There is a parturition heat 48 hours after the young are born (3). The average litter size is 9.6 (4); and the first litter is usually injured at parturition owing to the narrowness of the pelvis (2). The period of gestation is 135 to 150 days (5).

During the glandular proliferation of the uterus compact cellular nests proliferate toward one side of the existing glands and bud inwards to produce the complex progestational pattern (6). The anterior pituitary contains very little L.H. (7).

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HYRACOIDEA

PROCAVIIDAE

Procavia capensis Pallas

ROCK DASSIE

THIS South African dassie has a pedunculated corpus luteum (1). Pooled data on the number of embryos (2,3) gave a mean of 2.44 ± .054, with a mode of 2, and a range from 1 to 6. The young are born in November and December (3). The gestation period (observed) is 7½ months (4).

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Other PROCAVIIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	HABITAT, ETC.
Procavia (*Dendrohyrax*) *arborea* A. Smith Tree Dassie	No particular season (Shortridge)		1–2, rarely 3	Africa
P. syriaca Schreber	In Giza Zoo, once a year (Flower). No particular season (Shortridge)	In Giza Zoo, born mostly late March (Flower)	2–3, mean 2.6	N. Africa

PROBOSCIDEA

ELEPHANTIDAE

Elephas maximus L.

INDIAN ELEPHANT

THE Indian elephant is said to be polyestrous, and in captivity estrus lasts for 3 to 4 days (1). The young are born, one usually and rarely twins, from September to November, with a few at other times (2). The gestation period varied from 607 to 641 days in 6 observed cases, with a mean of 623.5 days. An average of 25 cases gave 21 months, 3 days, with a range from 17 to 24 months (3).

The age at puberty is variously stated. One record shows that a male and a female were 9 and 8 years old respectively (4), another that a male rutted at 15 years and a female calved at 13 years (5). More extensive records give 14 to 15 years for the male, and a calving age of 15 to 16 years for the female (6).

In the wild the preorbital glands of the male swell chiefly from November to February (7). A male elephant which was dissected had testes, which are inguinal, weighing 2 kg. each. The seminal vesicles contained 1.5 liters of an opalescent gray fluid. The penis had no prepuce. The head length of the spermatozoa averaged 8.3 μ, and the tails about 42 μ (8).

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Elephas (Loxodonta) africanus Blumenbach

AFRICAN ELEPHANT

In South West Africa the mating season is in January and February. One young is born, usually in June, and the female receives the male 5 to 6 months after calving (1). Gestation is about 21 to 22 months long (2).

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SIRENIA

DUGONGIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Dugong (*Halicore*) *dugon* Müller Dugong	Winter (Anderson)	1	1 year	Indian Ocean

TRICHECHIDAE

Trichechus manatus L. Manatee		1, rarely 2		Atlantic Ocean

ARTIODACTYLA

MUCH more work is needed before one can make many generalizations regarding reproduction in Artiodactyla. In general, it may be said that species living in temperate regions tend to be seasonally monestrous or seasonally polyestrous, but in the tropics reproduction may take place at any time of the year. There are, however, many exceptions.

In Cervidae, the deer, species from temperate regions are seasonally monestrous, breeding in late fall or winter in most cases, but tropical species tend to breed at any time of the year, even when they are brought into temperate regions. It is not clear whether they are monestrous or polyestrous in the tropics, and more information is needed on this point. Although growth of the antlers does not appear to be directly under the control of the testes, as it occurs in the castrated buck, these organs are necessary for their orderly development; for the reorganization of the spongy antler tissue into hard bone and for the shedding of the velvet, which lead eventually to their casting. Work is needed upon the influence of individual hormones, tablets of which might be implanted in males and females. Can antler development be induced in females? * Would early injection of testosterone cause premature hardening and shedding? What seasonal rhythm occurs in the testes of antlered "does," which are relatively common?

In tropical species the antlers are shed at any time of the year, but this is said not to occur annually in all species. Possibly each individual has its own rhythm of testicular activity.

In the Bovinae all species investigated tend to be polyestrous throughout the year, but in their natural habitats they probably all breed at a fairly definite time. The Caprinae, sheep and goats, are seasonally polyestrous,

* Dr. G. Wislocki has recently shown me the skull of a doe which possesses antlers grown under the influence of implanted testosterone pellets.

mainly in the fall, but some breeds of sheep have a much more extended season than others. In general, antelopes breed at any time of the year, but this may not be true of the Neotraginae, the pygmy antelopes, and of the Alcelaphinae, the hartebeests and gnus.

The Bovinae and, to a lesser extent, the Caprinae are remarkable for the low level of sex hormone production and excretion which seems to prevail, though more information is desirable on these factors in all mammals. At present they are certainly at the bottom of the list.

HIPPOPOTAMIDAE

Choeropsis liberiensis Morton

PYGMY HIPPOPOTAMUS

The pygmy hippopotamus breeds all the year round at intervals of about a month. Heat lasts for 3 days and the act of mating about an hour. The duration of gestation is from 201 to 210 days, and the female comes in heat again 12 to 16 days after the young have been weaned (1).

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Hippopotamus amphibius L.

HIPPOPOTAMUS

The hippopotamus breeds all the year round in captivity with regular heats a month apart (1). The number of young at a birth is 1. Combined data on the duration of gestation gave a mean value of 237.4 ± 1.2 days.

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TAYASSUIDAE

Pecari angulatus Cope

PECCARY

The peccary probably breeds in June in Panama, and the number of young is usually 2 (1). The uterus is bicornuate with relatively short and coiled cornua. The oviducts are short and coiled, and the fimbria form well-defined leaflets. The ovaries are not encapsulated. The old corpora lutea seem to persist much longer than is usual, since two sets of two each were found during pregnancy. The larger ones, 10 mm. in diameter, contained two cell types, large cells with dense cytoplasm, and much smaller cells with less dense cytoplasm. The smaller corpora lutea, 7 mm. in diameter, consisted mainly of the second type of cells, but they stained more deeply than they did in the larger corpora lutea (2).

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SUIDAE

Sus scrofa L.

DOMESTIC PIG

The pig has a cycle of about 21 days, which recurs all the year round. The duration of heat is about 2 to 3 days. Ovulation is spontaneous. Heat does not occur during lactation. The changes in the reproductive tract are not great, but, owing to the ease of obtaining material, excellent accounts, some of which are classical, have been written on the cyclical changes. The sow occupies an intermediate position among the domestic animals in regard to gonadotrophic hormone content of the pituitary. The duration of gestation is about 112 to 115 days. Many hermaphrodites are found in this species.

THE ESTROUS CYCLE

The length of the estrous cycle in the sow has not received as much attention as it has in other domestic animals, and statements of the mean lengths of the parts are, therefore, somewhat lacking in precision. The mean cycle length is 21 days, with a standard deviation of 2½ days (1). The modal length is 20 to 22 days (2). In South Africa, as in Europe, the cycles extend throughout the year; in Europe their average length is 21 days and in South Africa, 19 days. The length of the heat period is 2 days. Ovulation can occur on either day of heat, but it is more frequent on the second day (3). Observations made on 25 Poland-China gilts gave a cycle length of 21 to 22 days, and a heat period from 40 to 46 hours long, before they produced their first litters, and 65 hours long afterwards (4). A slaughter experiment showed that in 7 sows killed before 30 hours from the beginning of heat no follicles had ruptured, but when killed at from 30 to 36 hours, 6 of 7 sows had ruptured follicles, though the process was not complete in all cases (5).

The time of ovulation has been studied, not only by the method of slaughter and observation, but also by the use, at definite intervals, of double matings involving two inherited colors. By this means it was found that most eggs are shed at about 36 hours from the onset of heat and that all have been shed by the forty-eighth hour (6). Another similar study gave much the same results (7).

The left ovary appears to be slightly more active than the right. Observations on 14 sets of corpora lutea gave a mean ovulation rate of 15, of which 51.9 per cent were shed from the left ovary (8). A more extensive series which included 469 sows gave 55.3 per cent of ovulations from the left (9).

Heat does not usually occur during lactation, but it rapidly follows weaning. The mean length of the interval is 7 days, and it tends to be 1 day longer if the lactation is of short duration (1). The age at first heat averages 207.8 days, or 189.5 lbs. of weight, in small-type pigs, and 198.7 days, or 199.3 lbs. of weight, in large-type pigs (10).

Matings a few hours after the onset of heat were 63.0 per cent fertile, while those made on the second day were 65.8 per cent fertile (11). Matings made the day after the sow had gone out of heat were 20 per cent fertile, and later matings were completely infertile (5).

The rate of travel of the ovum through the oviduct has been worked out on material in which the oviducts were divided into five parts. The number of eggs in each part was obtained and expressed as a percentage of the whole.

As the average time for the complete passage is 3 days (12), this percentage gave an approximate idea of the rate of travel in the different portions of the tube. Passage is rapid through the first two-fifths, very slow through the next two-fifths, and rapid through the last fifth (13). This method probably gives too short a duration for the first part of the travel owing to a time lag in obtaining the specimens after slaughter, but the error is not great enough to invalidate the general conclusion.

The fecundity of the sow varies much with the breed. The litter size of the wild pig is said to be usually 4 (14), and from this low point the averages extend to 12.0 for the Large White Yorkshire. Climate or some other environmental factors influence the fecundity, since in the Philippine Islands several breeds average from 1 to 2 pigs less than they do in the United States (15). Young pigs have smaller litters than older ones; the maximum fecundity is reached at the fourth to sixth litters. The first litter averages about two less than the maximal size (16,17). This is partly due to the age of the sow, since those having their first litters at the usual age average one less than those littering for the first time a year later. It has been found in the rat that reproduction is, in itself, a stimulus to fecundity, and this seems to be true also for the pig, as those which have been continuously reproducing are more fecund than those of the same age which are producing their first litter. An interval of 9½ to 10½ months between the first and second litters increases the litter size by 1.6 pigs over sows with an interval of 4½ to 5½ months between litters, but the difference is not statistically significant. Litters born in the early spring tend to be larger than those born at other times of the year, and the smallest litters are those produced toward the end of the year (18).

One of the major problems in pig breeding is the wastage caused by loss of eggs and by fetal atrophy. This may be as high as 33 per cent or more. There is some reason to believe that it may be largely due to the action of genetic factors (42). Another is the number of stillborn pigs. The loss from this cause averages about 6 per cent. It is greater in litters with prolonged farrowings, and most of the dead pigs are born in the second half of the litter to be farrowed. Many of them have attempted to breathe but have smothered while they were still in the uterus. There is some evidence that the incidence of stillbirths may be reduced by an injection of pituitrin when farrowing begins (37).

The duration of gestation shows a difference with the breed, but the average for the lowest recorded, Middle White, 112.1 $\pm$ .6 days, is not far from the

TABLE 5. Litter Size of Pigs

BREED	AVERAGE LITTER SIZE	OTHER DATA
Imeretian (19)	6.6	
Kakhetian (19)	6.7	
Mangalita (20)	6.8	
Turopolje (21)	6.92 ± .04	S.D. = 1.43
Berkshire, in U.S. (16)	7.4	
Tamworth, in U.S. (22)	7.4	
Poland-China (23)	7.9	
Hannover-Braunschweig Landschwein (24)	8.0	
Golebska (25)	8.2	
Berkshire, in U.S. (23)	8.4	
Berkshire, in Europe (26)	8.5 ± .1	
German Large White (27)	8.9 ± .1	S.D. = 1.8. 85 per cent between 7 and 11
Hampshire (23)	9.1	
Livensky (28)	9.3	
Berkshire, in N.Z. (29)	9.3 ± .08	S.D. = 2.48. Mode, 9. 75 per cent between 8 and 11
Improved Spotted Mirgorod (30)	9.4	
Tamworth, in N.Z. (29)	9.4 ± .05	S.D. = 2.20. Mode, 10.75 per cent between 8 and 12
Machen (31)	9.6	
Danish Landrace, in U.S. (22)	9.74	
Chester White (23)	9.8	
Large Black, in N.Z. (32)	9.9	
Duroc Jersey (23)	9.9	
Mirgorod (33)	10.0	
Edelschwein (34)	10.0	
Edelschwein (35)	10.1	
Breitovskaja (36)	10.1	
Tamworth, in U.S. (23)	10.1	
Chester White (37)	10.1 ± .25	
Landrace (38)	10.2	
Improved Landschwein (35)	10.3	
Berkshire, in U.S. (37)	10.5 ± .3	
Duroc Jersey (37)	10.6 ± .3	
Wessex Saddleback (39)	10.6	
Swabian Halle (40)	10.9	
Large White (38)	11.0	
Norwegian Landrace (41)	11.2 ± .3	

S.D. = standard deviation.

highest, Berkshire, 115.4 ± .25 days (43). All the data is in agreement on this point, and it is hardly worth while further to summarize the data. However, the wild pig is said to have a mean gestation period between 127 and 128 days (44). The mode for domestic pigs is close to the mean, the standard deviation is usually about 3 days, and the differences for age of sow, litter sequence, and litter size are not significant (45). Seventy-three per cent of farrowings occur between 2 P.M. and 4 A.M. (46).

The sex ratio of pigs at birth is 49.56 per cent males for a large series of records. The sex ratio has attracted some attention because it has been found that stillborn pigs have a much higher ratio of males, while that for fetuses increases at the younger ages. Extrapolation of the curve of fetal sex ratios suggests a ratio at conception of 60 per cent males, sufficiently remote from the equality demanded by current genetic theory to be interesting (47). The phenomenon is, as yet, unexplained. Another unexplained peculiarity of the sex ratio is that more litters with nearly equal proportions of the sexes are born than would be expected if the results were due to chance (48).

HISTOLOGY OF THE FEMALE TRACT

OVARY. Multilayered graafian follicles appear in the ovaries of the gilt at about 7 weeks of age. At 15 weeks vesicular follicles appear. The blood supply to the medullary region increases markedly when multilayered follicles appear, and to the theca externa of individual follicles when the antra are formed. Stimulation with gonadotrophes is without effect before vesicular follicles are present (49). In the breeding sow the follicles about to rupture measure 7 to 10 mm. in diameter. The granulosa layer is 6 to 9 cells deep and the theca interna is 0.09 to 0.1 mm. thick. The ripe follicles are clear and semitransparent and stand out from the ovary like a bunch of grapes. When the follicle ruptures, a considerable amount of liquor folliculi escapes and the follicle collapses. There is a slight eversion of the granulosa and theca interna and a slight oozing of blood. The membrana propria breaks down, with the result that the sharp line of demarcation between granulosa and theca is lost. The latter grows inwards, starting at the apices of the folds into which it has been thrown by the contraction of muscular fibers in the theca externa. The thecal cells divide by mitosis, and the granulosa cells enlarge. By the seventh day of the cycle the corpora lutea measure 8 to 9 mm., and in the second week their maximum size of 10 to 11 mm. is reached. Degeneration of the corpus luteum is rapid at the end of heat and at parturi-

tion (50). At first the corpus luteum is pinkish in color, but at the end of diestrum a rapid change takes place with the degeneration of the capillaries, and the color becomes a primrose yellow, changing to yellow-brown as resorption advances. The cellular changes in the corpus luteum of pregnancy have been described in great detail (51).

There is a double wreath of blood vessels in the theca externa and theca interna. That of the theca interna grows directly into the granulosa at ovulation, but that of the theca externa merely enters the developing corpus luteum in the folds of tissue. No lymphatic vessels are present until 2 days or more after ovulation; these structures are the first to degenerate and are not found later than 16 to 17 days after ovulation. The capillaries and venules are the next to degenerate (52).

VULVA. During diestrum the labia are contracted, the muscles are tight, and the walls are pink and moist. The latter swell during early heat and become red internally. Late in heat they become flabby, the muscles are fully relaxed, the mucosa is still red, and some mucus is present. During metestrum the labia revert to the diestrous state, but a good deal of mucus is present (8).

VAGINA. During diestrum the basement membrane of the epithelial layer is indistinct; there are 3 to 6 layers of cells with but few leucocytes between them. In early heat the basement membrane is distinct, the epithelial layer is actively growing and is now 10 to 15 cells thick, with low columnar cells at the surface. Blood vessels are distended and the stroma is edematous. In late heat the basement membrane has again become indistinct, the number of layers of epithelial cells has increased to 14 to 26, cornification is evident, and leucocytes have wandered between the cells. During metestrum desquamation is in evidence, and leucocytes are abundant, but cornified cells are not present in great numbers. Many of the cells show vacuolar degeneration (8,53).

The vaginal smear is not a good indication of the reproductive state. There is more mucus during heat, especially late in the period, and the proportion of leucocytes tends to increase. In early diestrum many of the epithelial cells are vacuolated, more so than at other times (53,54).

UTERUS. The uterine stroma becomes edematous in late diestrum. This increases during proestrum, becomes less intense during heat, and rapidly disappears during metestrum. Leucocytes are to be found at all stages but are more frequent from late diestrum to 4 days postestrum. The epithelial cells grow and become pseudostratified, owing to the crowding of the nuclei, during proestrum and continue in this state to about 1 week postestrum.

They show vacuolar degeneration during proestrum but have become normal in appearance by late heat. Cilia are present only in the crypts and glands (8,12). They do not appear to fluctuate in numbers during the cycle (55).

The oviduct enters the horn of the uterus as a continuous passage, i.e., without any angle. There is no sphincter, but the mucosa projects in a number of fingerlike folds. The whole structure is like a rosette with the oviduct opening through the center. These projections are edematous just after heat, and at this time the pressure needed to force fluid from the uterus into the oviduct increases from 50 to 155 mm. of mercury. The pressure needed to force fluid from oviduct to uterus varies only slightly. It is about 25 mm. of mercury (56).

The ciliated epithelium of the oviduct is 25 μ high during and just after heat; it declines to 10 μ in the second week of diestrum and then gradually grows to the maximum during the third week. The nonciliated cells are smooth in the first week of the interval, and in the second numerous cytoplasmic processes, like those described for other species, including the cow, are extruded (57).

PITUITARY. During the heat period the basophilic cells of the anterior pituitary lose their granules, which were abundant during proestrum. They also contain many granules during the early lutein phase, but not in the middle and late lutein phases. Degranulation of the eosinophils also occurs during heat (58). The gonad-stimulating hormone can first be detected in the anterior pituitary of the fetus at a crown-rump length of 17 to 18 cm. (59). Its appearance coincides with a large increase in the number of basophilic cells (60).

PHYSIOLOGY OF THE FEMALE TRACT

The uterine muscle of the sow has been intensively studied. During heat there is great spontaneous activity. Two kinds of contractions are found, large ones at intervals of 1.5 to 2.5 minutes, with superimposed smaller contractions of short duration. During metestrum (tubal ova) they are more irregular, and the minor waves are more pronounced than the major ones. In mid-diestrum the irregularity has increased, and the short waves are even more in evidence (61,62). The muscle uses most oxygen at 3 days before ovulation, and least at 4 to 18 days after ovulation (63). The muscle contracts in response to pituitrin and relaxes to adrenalin at all stages of the cycle (64).

The muscle of the oviduct is most active during, and just after, heat (65). At this time the contractions occur about 13 to 15 per minute as measured during insufflation. In diestrum they occur 5 to 9 per minute, but their amplitude is greater (66).

Intra-uterine migration of the ova is a usual phenomenon in the sow. If one ovary is removed, 42 per cent of the embryos which develop are found in the horn of that side. There is also a tendency in the normal sow for the number of embryos on each side to be equalized (9).

The estrogen content of large graafian follicles is about 900 R.U. per kg. of liquor folliculi, while corpora lutea contain from 25 to 78 R.U. per kg. (67). The occurrence of estrogenic substances in the urine during pregnancy is peculiar. From 19 to 30 days 1,000 to 3,000 M.U. per liter are found, their first appearance being rather sudden. Then they disappear almost entirely, to reappear about the seventieth day. After this they rise gradually in amount and just before parturition 5,000 to 10,000 M.U. per liter are found. After parturition they disappear rapidly. These facts have been amply confirmed (68–70). The content of chorionic tissue exactly parallels that of the urine, though at a lower level (71), and the gonadotrophic hormone content of the pituitary is in inverse relationship. This is highest during proestrum, falls abruptly at ovulation, and is very low during diestrum. During pregnancy it reaches a maximum from 30 to 75 days (72). These relationships raise some interesting questions which deserve further study.

The corpus luteum contains appreciable quantities of progesterone during the first 3 days after ovulation, before the lutein cells are fully differentiated. The content rises until 15 days, after which it falls abruptly and soon cannot be estimated. During pregnancy it rises rapidly to 20 days, then continues to rise slightly to 105 days, after which the fall is rapid (73).

The anterior pituitary contains less F.S.H. than that of the horse, but more than that of the sheep. In L.H. content it is variable, but it is always below that of the sheep (74,75).

Tables have been constructed giving the prenatal growth of pigs (76).

THE MALE

Primary spermatocytes first appear in the testes at about 84 days and secondary spermatocytes at 105 days, and by 147 days spermatozoa are present (77).

The two testes are about $\frac{1}{250}$ of the body weight at maturity, the left

usually being the larger; and the epididymides are about ⅓ the weight of the testes. The vasa efferentia number from 1 to 5, and the vas deferens is about 25 to 30 cm. long (78). The length of the epididymis of a Mangalita boar was 62 to 64 metres, and the number of efferent ducts was 8 to 12 (79). The accessory glands are very large, the seminal vesicles weigh from 151 to 844 g. when full, and the contents weigh 39 to 507 g. Cowper's glands weigh 146 to 209 g. when empty, and the contents, 20 to 178 g. The prostate weighs 15 to 26 g. The boar also possesses a disseminate gland not at all like the prostate in structure, but in close proximity to it (78).

Coitus take 5 to 8 minutes, and the average volume of ejaculate is 255 cc. (80). The semen penetrates directly into the cervix during mating (81).

The average ejaculate contains about 85 billion spermatozoa. Ejaculation occurs in stages; it increases to the third minute and is maintained to 5 minutes, then there is a fall in the rate and a final rise. Most spermatozoa are found in the first ejaculate. Ejaculation at 24-hour intervals does not materially reduce the volume, but greater frequency does. The pH of normal semen is 7.3 to 7.8. If it is allowed to stand, a large quantity of gelatinous and waxy materials settles out. This gelatinous material is secreted partly by the vesiculae seminales. Removal of these glands has little effect upon the number of spermatozoa, although the glands provide about 25 per cent of the ejaculate. Cowper's glands secrete the waxy material, and their secretion reacts with that of the seminal vesicles to produce the gelatinous material. They provide about 19 per cent of the total ejaculate. Without either seminal vesicles or Cowper's glands, the boar produces a watery, thin semen containing no gelatinous or syrupy material. The prostate and urethral glands produce about 56 per cent of the total secretion. This is clear and almost as thin as water. The testes produce about 2 per cent of the total volume (78).

Removal of Cowper's glands, or of the seminal vesicles, or both, is without effect upon fertility (78), in contrast to the condition found in the rat.

A few points of interest in the composition of these secretions follow:

Vesiculae seminales, pH 6.4 to 6.8, relatively high in K and glucose, low in Cl.

Cowper's glands, pH 7.2 to 7.3, relatively high in Na and Ca, very high in Mg.

Epididymal secretion, pH 6.7 to 6.9, high in P.

Prostate and urethral glands, pH 7.5 to 8.5 (78).

The head size of the spermatozoa averages 8 μ (82).

The cryptorchid testis contains 1 B.U. of androgen to 87 g. of tissue, and

the normal testis contains 1 B.U. to 39 g. (83). The following levels of gonadic hormones have been found in the urine: androgens, 90 to 134 M.U. per liter; estrogens, 1,170 to 1,640 M.U. per liter (84).

Castration at 200 days of age, after the accessory organs have grown somewhat under the influence of androgens, does not produce organs as small as those which result if the operation is performed at 50 or 100 days (85).

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Other SUIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Sus cristatus Wagner Wild Pig	End March (Brander)		4–6	4 months	India
S. gigas Heude Manchurian Wild Pig	No fixed season (Sowerby)		6		Manchuria. 1 record
Babirussa babyrussa L. Babirusa				125 days, 150 days	Celebes
Potamochoerus larvatus Cuvier African Bush Pig		Dec.–Jan.	5–8		S. Africa
Hylochoerus meinertz-hageni Thomas				125 days	Kenya
Phacochoerus aethio-picus Pallas Wart Hog	Late June early July (Hubbard)	Oct.–Nov.	Usually 4	171–175 days	Africa. Breeding data and gestation period do not quite fit

CAMELIDAE

Camelus bactrianus L.

BACTRIAN CAMEL, TWO-HUMPED CAMEL

The bactrian camel is polyestrous, having cycles all the year round. These are variable in length; the usual interval between heats is from 10 to 20 days; and the duration of heat 1 to 7 days, with a mode of 3 to 4 days (1). The mean cycle length is about 14 days, and the foal heat is experienced the day after calving, more rarely after 2 to 3 days. The suckling female comes in heat regularly but the duration is shorter than it is in the dry camel (2).

At the beginning of heat the graafian follicle measures from 1 to 1.5 cm. in diameter, and at ovulation it has grown to 2.5 to 3 cm. The optimum time of mating is from 3 to 5 days before the end of heat. There is little obvious change in the appearance of the vagina and cervix during heat, but the vaginal smears show a decrease in leucocytes and an increase in epithelial cells (2).

The mean duration of pregnancy in 850 cases was 406 days with a spread from 370 to 440 days, calculated from the last mating. From single matings the mean was 410 to 411 days. One young is usually born at a time, and males are carried for 2 days longer than the females, but this difference is not statistically significant (3).

Both the males and females have well-developed glands at the summit of the neck, just below the occiput. In London these are active in March in the males, but the glands of the females are not noticeably active during the breeding season (4). Rut in London and in Mongolia is in spring (5).

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Other CAMELIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Camelus dromedarius L. Dromedary		1	12–12½ months	Glands on neck below occiput active in both sexes during June in London (Pocock)
Lama glama L. Llama	Summer and early fall (Nov.–May) (Cabrera and Yepes)	Usually 1	11 months	S. America
L. g. huanacus Molina Huanaco	End of spring, Nov. (Cabrera and Yepes)	Usually 1, occasionally 2		S. America
L. vicugna Molina Vicuña	All year, mostly Apr.–June (Cabrera and and Yepes)	1, rarely 2	10 months	S. America

TRAGULIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD
Tragulus javanicus Osbeck Little Malayan Chevrotain			1–2	
T. meminna Erxleben Indian Chevrotain	June–July (Blanford)	At close of rains	2	120 days

CERVIDAE

Capreolus capreolus L.

ROE DEER

The roe deer is monestrous, mating in July and August, and the fawns, usually twins, are dropped in May (1). Implantation is delayed, the only case so far known in Cervidae. The period of gestation is about 40 weeks, with implantation of the embryo in December, but exceptional cases are known of immediate implantation with a reduced gestation period of 20 weeks (2). The time of breeding is exceptional among deer, but implantation and birth are at about the usual time.

The antlers begin to grow in January and are shed in December (3). Castration before the velvet has been shed is not followed by casting of the antlers, but their further growth is abnormal; castration after the velvet has been shed leads to immediate casting and the growth of abnormal forms. Ovariectomy of the female does not result in any antler growth (4).

The testes begin to grow in the spring and to retrogress in the fall, receding to one third of their weight at the height of the breeding season. Spermatogenesis is said to begin in the spring and to cease about October (5).

A castrated stag had incipient peruke formation. After two injections of 50,000 M.U. of progynon the growth began to shrink and it was shed. It began to grow again in August and September, although it was not the normal season for growth (6). Injections of 50,000 M.U. of progynon at 7- to 10-day intervals in October and November caused an immediate onset of growth; the velvet dried and the antlers were shed in December (7).

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Cervus (Axis) axis Erxleben

SPOTTED DEER, CHITAL

In the wild state in India the chital breeds at any time of the year, but there is a distinct rutting period at the end of April or the beginning of May. Corresponding with the extended breeding season is the fact that the antlers are shed at any time, but mostly in August (1). In captivity a continuous series of diestrous cycles lasting for 3 weeks is experienced throughout the year (2), and at Woburn, England, chitals will breed at any time of the year (3).

The number of young is usually 2, but 1 and 3 are not uncommon, and the doe may produce two families in a year (1). The period of gestation is 7 to 7½ months.

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Cervus canadensis Erxleben

WAPITI, ELK

In the wild the wapiti ruts from late September well into October, and the young are born in June. In captivity the female experiences a continuous series of diestrous cycles lasting 3 weeks, and pregnancy at all times is only prevented by the fact that the males do not rut during the casting and growth of the antlers (1). These are shed in mid-March and they begin to grow again immediately. The velvet is lost in August (2). One young is usually born at a time, but occasionally 2 and 3, and the gestation period is about 8½ months.

A two-year-old elk was castrated; the antlers were shed and new ones soon grew. These were small and crooked; they never lost their velvet or were shed (3).

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Cervus (Rusa) unicolor Bechstein

SAMBAR

The period of rut in the sambar is from October to November in the Peninsula of India, but possibly in the spring in the Himalayas. The antlers are said to be shed in March in the Peninsula and in April in the Himalayas, but the time is variable (1). According to one account they are not shed annually but about every 3 to 4 years, at any time of year. Fawns are dropped and antlers are shed at any time of the year at Woburn, England (2). There is a record of shedding in the Washington, D.C., Zoo on June 18 (3). The facial glands enlarge during rut. One to two young are usually born at a time, and the period of gestation is about 8 months (4). Birth is usually late in May or early in June in the sambar's native habitat (5).

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Odocoileus hemionus Rafinesque

MULE DEER

The mule deer ruts from November to mid-December, and the fawns are born in May and June. The antlers are shed in March. During rut the neck swells. The usual number of fawns is 2, rarely 1 or 3 (1). Puberty is usually at 4 years of age in the male (2).

Castrated bucks either do not renew their antlers or retain them permanently in the velvet with remarkable distortions. They are known locally as "cactus bucks" (1). The tarsal and metatarsal glands of the males are markedly more active during rut than at other times. An antlered "doe" sheds her antlers and grows them at the usual time for the male. Her neck

swells during the rutting season; she attacks bucks in rut and attempts to mount a doe (3). Evidently this is a male pseudohermaphrodite.

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Odocoileus virginianus Boddaert

WHITE-TAILED DEER, VIRGINIA DEER

In the northern part of its range the white-tail mates in November, but in Florida mating is earlier. In the north the young are born late in May and June; in the south they are born from January to March. The males shed their antlers in the north from late December to February, and earlier in the south (1). They begin to grow again after an interval of 2 to 6 weeks, and the velvet is lost in August and September. Rut, lasting about 2 months, is accompanied by swelling of the neck (2). The number of young is usually 2, and the gestation period is about 7 months.

Deer are fall breeders, but, if their reproduction is controlled by a reduction in the daily amount of light, as is believed to be the case with many of the mammals which are in this class, one would expect breeding to be later as one goes further south in the range, instead of earlier. Probably some other factor or factors are involved in this case.

The weight of the testes fluctuates seasonally, being greatest at the time of rut and least from late winter to early summer. Spermatogenesis begins in July, is maximal in October, and diminishes in December and January. The lowest point is reached in June when the seminiferous tubules consist of a single layer of cells. Interstitial cells are larger and have clearer nuclei in October than in May and June. The prostate complex shows no seasonal variation, but the seminal vesicles are least in size in June and July, enlarge in August, and are maximal in October. The height of the secretory cells follows the same rhythm. Secretion is abundant in October, whereas the lumen of the gland contains black dried masses in June and July (3).

The antlers begin their annual growth when the testes and accessory organs are inactive, harden and lose their velvet when these glands are enlarging, and are shed when they begin to decline (3). Castration following

loss of the velvet results in shedding within 30 days. New growth, which occurs at the normal time, is abnormal in shape, and the velvet is not lost. Growth ceases at the usual time and part of the growth, being somewhat fragile, may be lost by accident. Renewed growth activity follows in the spring. Eventually an exaggerated burr is produced (4). These events have been interpreted as indications that antler growth is under the influence of a nontesticular hormone, possibly from the anterior pituitary, though direct evidence for the latter is lacking. Hardening and consequent loss of the antlers is believed to be due to the action of a testicular hormone (3). If antler growth were caused by a nontesticular hormone, it might be expected to occur in the female, which it does not. A genetic explanation would, in the present state of our knowledge, be simpler. Transplantation of antler buds might help unravel the problem.

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Rangifer tarandus L.

REINDEER, CARIBOU

There are many races of the reindeer, some of which have been given specific rank. In this account Lydekker's classification has been followed. This groups them all into one species, but, where possible, the subspecies has been indicated. Both sexes are antlered and shed annually.

The breeding season in Siberia is in September and October, and the calving season is from May to June. The males breed first at 1½ years of age. Normal bucks shed their antlers from November to January, and castrated ones from March to April (1). The number of young is usually 1, rarely 2, and the period of gestation is from 7 to 8 months (2). These remarks presumably refer to *R. t. sibiricus* Schreber.

In *R. t. caribou* Gmelin, the woodland caribou of North America, rut is in October. The males shed their antlers in early spring and the does in summer (3).

In *R. t. arcticus* Richardson, the barren-ground caribou of North America, rut is in October and the calving season is from May 15 to June 15. The bucks usually shed their antlers in November, but old and very young ones may carry them until late April. The does usually shed in May and June (4). The velvet is rubbed off beginning in August, and the antlers are clean by the end of September. Antler growth begins in May, even though they may have been shed in December (5).

Authorities are agreed that castrated or ovariectomized reindeer shed and regrow their antlers each year, contrary to the habit in other deer which have been investigated (6).

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Other CERVIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Alces alces L. Elk. Moose (= *A. americana* Clinton)	Mid-Sept. to mid.-Oct. (Hamilton, Lydekker)	Late May	Usually 2	240–250 days	Antlers shed Jan.–Feb. in N. America; begin to grow Apr.; velvet shed July–Aug.
A. gigas Miller Alaska Moose		May (Cahalane)	Usually 2		Alaska
Blastocerus bezoarticus L. Pampas Deer	End of summer (Cabrera and Yepes)	Sept.–Oct. in Matto Grosso; Apr. in Argentina	1		Sheds antlers in May in Brazil
B. dichotomus Illiger Marsh Deer		Oct.–Nov. (Cabrera and Yepes)	1	About 1 year	S. America

Other CERVIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Capreolus bedfordi Thomas Manchurian Roe Deer	July (Sowerby)	Late May or early June	Usually 2		
C. pygargus Pallas Siberian Roe Deer	Sept. (Lydekker)				
Cervus cashmiriensis Adams Hanglu	Oct. (Blanford)	Apr.		6 months	Antlers shed in March in Kashmir; records of Apr. shedding in U.S.
C. elaphus L. Red Deer	Sept.–Oct. Very extensive series of cycles in captivity (Heape)	May–June	1, rarely 2	Av. 234 days	Sheds antlers March–May
C. macneilli Lydekker	End Oct.–Nov.				W. China. Antlers shed April
C. wallichi Cuvier Shou				6 months	Tibet
C. (*Hyelaphus*) *porcinus* Zimmermann Hog deer	Sept.–Oct. in India (Blanford). In England all year (Bedford and Marshall)			8 months	Sheds antlers Apr. in India; records of Feb. and July in zoos (Philadelphia and Washington)
C. (*Rucervus*) *duvauceli* Cuvier Barasingha	Monestrous; rut ill-defined; Dec.–March,	Spring	1	250 days	Antlers shed Jan.–Feb. in India; records of Dec., Jan., and

Other CERVIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
	but mostly Dec. 15–Jan. 15				Apr. in U.S. Said to mate end Sept. to end Nov. in Kashmir (Heape)
C. (Rucervus) eldi Guthrie Thameng	March–May in Burma (Blanford), also in England	Oct.–Nov.	1	183 days	Antlers shed June in Manipur; Sept. in Lower Burma. Puberty at 18 months
C. (Sika) nippon Temminck Sika			1	Av. 222 days	Japan. Records of antlers shed March, Apr., May in U.S.
Dama dama L. Fallow Deer	Sept.–Oct., monestrous (Lydekker)	June–July	Usually 1, rarely 2	Av. 230 days	Neck swells during rut. Antlers shed May
Elaphurus davidianus Milne-Edwards Père David's Deer	In England, June–July (Lydekker)		1–2	250 days	Originally China; only known in domestication. Antlers shed Nov.–Dec.
Hydropotes inermis Swinhoe Chinese Water Deer			2–5, 3 and 4 common		N.E. China and Korea
Mazama americana Erxleben Red Brocket	No known fixed season (Cabrera and Yepes)	Dec.–Apr., July	1		S. America
M. simplicicornis Illiger Wood Brocket			2		S. America

Other CERVIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Moschus moschiferus L. Musk Deer	Jan. (Blanford)	June (Lydekker)	1	160 days	Cent. and N.E. Asia. Puberty at less than 1 year (Blanford)
Muntiacus muntjak Zimmermann Muntjac	All year, more frequently Jan.–Feb.		1–2	183 days	Sheds antlers May. S. Asia
M. reevesi Ogilby	All year at Woburn (Bedford and Marshall)				E. China
Odocoileus columbianus Richardson Black-tailed Deer	Oct.–Nov. (N.A.F. 55). Monestrous	May–June	1–3		Sheds antlers Jan.–Feb. Western N. America

GIRAFFIDAE

Giraffa camelopardalis L.

GIRAFFE

The giraffe in the wild is said to mate from July to September and to drop her young from October to February (1). In captivity about three cycles in the breeding season have been observed (2). One young, rarely twins, is born at a time, and the period of gestation has been observed to be between 14 and 15 months.

Gonadotrophic hormones are present in the urine of the pregnant female (3).

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Okapia johnstoni P. L. Sclater

OKAPI

The period of gestation has been observed in one case as 426 days (1).

1. Kenneth, J. H. Gestation Periods. Imperial Bureau of Animal Breeding and Genetics, Edinburgh, 1943.

ANTILOCAPRIDAE

Antilocapra americana Ord

PRONGHORN

The pronghorn has a limited breeding season in September and October, and the horns are shed immediately afterwards, from October to December (1). The new ones have already begun to sprout (2). The young are usually born from late May to early June, though in Texas they are born over a wide range of time, but mainly in June. Records of young give 2 on six occasions, and 1 once (3). In view of the relationship of this species to both the antelopes and the deer it would be interesting to learn the connection of the testis cycle to horn shedding. A report on one animal states that in a castrated buck horn development was abnormal and that the seasonal separation of the horns was incomplete (4).

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BOVIDAE

BOVINAE

Bos taurus L.

DOMESTIC CATTLE

Domestic cattle are polyestrous, breeding all the year. Ovulation is spontaneous, and it occurs at intervals of about 21 days. The length of proestrum has not been accurately determined, but probably it lasts for 2 to 3 days. Estrus lasts for less than 1 day, and the cow goes out of heat before she ovulates. Frequently, more so in younger than in older cows, overt bleeding occurs from the uterus about 18 hours after ovulation. The corpus luteum is functional for about 19 days; its decline and proestrum are synchronous. Uterine changes during the cycle are not marked. The vaginal smear is not a very reliable indication of the reproductive state. The pituitary of the cow has the lowest recorded F.S.H. content; L.H. is also low, but prolactin is very high. The period of gestation is about 280 days; 1 calf is the rule, but more are frequently born. When a female is born cotwin with a bull, she is usually sterile as her gonads have been modified early in development. The bull produces spermatozoa all the year round.

THE ESTROUS CYCLE

There have been many investigations of the length of the estrous cycle in cattle (1–6). A summary of all the available data, which include a considerable series of records from the New York State Dairy Herd Improvement and Artificial Insemination Associations, gives a modal cycle length for unbred heifers of 20 days, and for cows, 21 days (6). The cycle length is less variable in heifers, in which 85 per cent fall between 18 and 22 days, but in cows 84 per cent fall between 18 and 24 days. The mean for heifers is $20.23 \pm .05$ days, and the standard deviation is 2.33 days. For cows the mean is $21.28 \pm .06$ days, and the standard deviation is 3.68 days. Although there is a definite difference in the cycle lengths of virgin and parous cattle, it cannot be said that the cycle increases in length with age, as analyses of

different sets of data have yielded conflicting results. The season of the year has no effect (5,6). There are indications that the individuality of the cow has some effect on the cycle length, but more evidence is needed on this point. All these figures refer to dairy or to dual-purpose cattle. For range (beef) cattle, Herefords, the length of the cycle is essentially similar (7). The mean cycle length for all ages of beef cows is 19.6 ± .12 days, the mode is 20 days, and 79 per cent fall between 17 and 23 days. In this group cows came in heat equally at all times of the day.

The duration of heat has not received as much attention as it deserves. A compilation from available data (1,8,9) gives a mean duration of 13.6 ± .16 hours, with a standard deviation of 3.9 hours. The modal length is about 14 hours, and 82 per cent fall between 10 and 18 hours. These figures are for cattle of all ages, but it has been shown (1) that heat lasts for a shorter time in heifers than in cows. It is not clear whether the duration of heat is affected by the season of the year.

Ovulation is spontaneous, and it usually occurs from 13½ to 15½ hours after the cow goes out of heat (9–11). There is, however, considerable spread, from 2 hours before the end of heat to 26 hours after it. About 80 per cent of ovulations occur between 4 P.M. and 4 A.M., a concentration partly brought about by a shortening of the interval between the end of heat and ovulation if the former ends close to this period of the day (11). Both dairy and beef cattle are included in this range. Heifers tend to ovulate about 3 hours earlier than cows (10). The right ovary tends to produce more ovulations than the left. A corpus luteum count showed 60.2 per cent in the right ovary (12), and an embryo count gave 60.5 per cent in the right horn of the uterus (13). This is an unusually large difference in ovulation rates. Removal of the corpus luteum brings the cow into heat 3 to 4 days afterwards in the majority of cases. The mean interval is 4.2 days (14).

The return of heat periods after parturition occurs after a very variable interval. For dairy cows a modal interval of 41 to 60 days has been reported (5), and a mean of 69 days, with a standard deviation of 39 days (15). For beef cattle the mode is 60 to 70 days, with 80 per cent between 20 and 160 days, and the mean, 80.2 ± 1.3 days (7). In this study it was found that the chance of conception at a heat period earlier than 40 days is only 49 per cent, but it rises until average fertility is reached at 70 days.

A little more than a day after ovulation bleeding occurs from the vulva in many cows. The source of this blood is discussed in the section on histology. It is more frequent in heifers (about 75 per cent) than in cows (48 per cent)

(16), but it does not occur at every heat period in any one individual; great variation is shown in this respect (6). There is much division of opinion among cattle breeders concerning the significance of the bleeding; some hold that it is a sign that the cow has not become pregnant, others that she has, provided she had been served. Recent work (17) showed that, of 100 heifers bred at heat, 81 bled; of those that conceived, 85 per cent bled; but of those that did not conceive, 74 per cent bled. In a similar group of 100 cows 61 bled, consisting of 69 per cent of those that conceived and 39 per cent of those that did not.

FERTILIZATION

As the egg is shed some time after the end of heat, it becomes important to know whether the cow can be bred successfully after the end of heat by artificial insemination and whether spermatozoa deposited in the female tract early in the heat period can survive until ovulation. The conception percentage for artificial inseminations at different times is given in table 6 (18,19). The figures show that the chance of conception with early services is smaller than with later ones, and that after 6 hours have elapsed from the end of heat it again becomes reduced. As the spermatozoa reach the upper third of the oviduct in 5½ hours in cows, or in 4½ hours in heifers (10), the reduction in fertility is marked if they are not at the top of the oviducts at the mean time of ovulation. This suggests a short life for the egg, a conclusion that has been reached for other species. It would appear, also, that the fertility of the spermatozoa is reduced after a stay of a little more than 24 hours in the female tract.

The ovum remains in the oviduct for 96 hours; in the first 6 hours it travels one-third of the distance, during which time it is fertilized. After this rapid passage the remainder of the journey is made at the rate of about 1 mm. per hour (20).

Twins are more frequent in dairy breeds than in beef breeds, the incidence being 1.88 per cent in the former and 0.44 per cent in the latter. Monozygotic twins account for 6.0 ± 1.9 per cent of the total. The chance of producing twins increases with the age of the dam to 8 to 9 years (21). A compilation of information in the Wurttemburg herdbooks gives a higher incidence of twins, ranging from 3.2 per cent for the spotted breed to 1.7 per cent for the brown breed. Triplets occurred in about 0.03 per cent of conceptions, and quadruplets in about 0.0004 per cent. Multiple births were

most frequent from 5 to 7 years of age (22). There is some seasonal variation in the incidence of twins. In dairy cattle it is highest in July and April, and lowest in January and June (21); in beef cattle in the United States it is highest in August and lowest in March (23). Fifty-seven per cent of twins are male and female (22), and of the female twins in this sex combination only 6 per cent are fertile (24,25).

The sex ratio at birth has been the subject of an extensive investigation (21), and it was found to be 51.52 ± .14 per cent males. The number of

TABLE 6. The Effect of Inseminating Cows at Different Times on Fertlity

TIME OF INSEMINATION	PER CENT FERTILE
Beginning of heat	44.0
Mid-heat	82.5
End of heat	75.0
6 hours after end	62.5
12 hours after end	32.0
18 hours after end	28.0
24 hours after end	12.0
36 hours after end	8.0
48 hours after end	0

the pregnancy had no significant effect except for the first calf, in which the ratio was 52.76 ± .49 per cent males. The ratio in abortions and still-births was 58.04 ± 1.58 per cent males, which suggests, in conjunction with the ratio at birth, that many more males are conceived than females. The sex ratio of fetal calves is somewhat variable, but the trend is toward a greater number of males in the younger feti (26). Multiple births tend to have a lower proportion of males (21).

The mean duration of gestation varies with the breed, and the range of the breed means is from 278 to 290 days. Some mean gestations are given in table 7. There is general agreement that males are carried about 1 day longer than females and that the gestation of twins lasts 5 to 6 days less than that of singles. A slight increase with the age of the dam up to 6 years of age, perhaps 2.5 days in all (28), has been generally noted, but the month of calving has little or no effect. There is little indication that birth is much more frequent at one time of day than another (44), though there is some suggestion that fewer are born during the early morning and evening (45).

TABLE 7. Mean Gestation Periods of Cattle by Breeds

BREED	DURATION OF GESTATION DAYS	OTHER DATA
Ayrshire (27)	277.84 ± .12	S.D. = 4.30
Jersey (27)	277.94 ± .23	S.D. = 5.48
Holstein (28)	278.15 ± .15	
Holstein (27)	278.27 ± .16	S.D. = 4.89
Jersey (29)	278.5	n = 1,075; 90 per cent from 271–285
Jersey (28)	278.9 ± .18	
Oldenburg Wesermarschvieh (30)	279.3 ± .2	S.D. = 4.74
Holstein (31)	279.9 ± .06	80 per cent from 273–286; singles only
Beef Shorthorn (32)	280.8	n = 164
Holstein (33)	281.0 ± .15	
Westerwalder (30)	281.4 ± .1	S.D. = 4.3
Montafon (34)	281.5	
Gray Bulgarian (35)	281.5	
Milking Shorthorn (32)	281.7	n = 133
Swedish Friesian (36)	281.85 ± .19	
British Friesian (23)	282	
Angler (30)	282.2 ± .2	S.D. = 5.4
Aberdeen Angus (27)	282.5 ± .2	S.D. = 3.60
Guernsey (33)	283.0 ± .46	
Sindhi (37)	283	
Swedish Red and White (38)	283.7 ± .06	S.D. = 5.8; mode = 283–284
Jersey (33)	284.3 ± .7	
Ayrshire (33)	284.6 ± .44	
Antioqueno (39)	285	
Red Poll (23)	285	
Hereford (27)	285.2 ± .15	
Norwegian (40)	285.8 ± .07	S.D. = 5.7
Mocho Nacional (41)	286.5 ± .58	
Caracu (41)	286.9 ± .35	
Ongole (42)	289.1	
Brown Swiss (43)	290	
Bernese (34)	290.1	

S.D. = standard deviation; n = number of observations.

HISTOLOGY OF THE FEMALE

OVARY. At birth the ovaries are in an advanced stage of development; vesicular follicles can be found in young cattle at all ages (46). The age at first heat is stated to vary from 6 to 18 months, with pronounced breed differences, but no precise data bearing on this point have been found. Large follicles, which have reached the usual maximum, 12 mm. in diameter, before the ovulatory increase sets in, are found in the ovaries of 6-month-old calves well before puberty (1). During the cycle follicles of this size, or a little larger, are found at 8 to 9 days postestrum and also during pregnancy (47). The maturation growth is made mainly during heat, and the size of the follicle at ovulation is 16 to 19 mm. (48). The histology of the developing follicle seems to have received little attention, but the changes during ovulation and the development of the corpus luteum have been described in detail (48).

In the mature follicle during heat the blood vessels of the theca interna, which is prominent in the cow, are distended, and there is a slight leakage of erythrocytes into the granulosa and into the outer part of the liquor folliculi. A few granulosa cells are already enlarged. Many leucocytes can be found in the follicle. At ovulation much liquor folliculi and the cumulus are emitted, but most of the granulosa remains. The theca externa contracts markedly, throwing the theca interna and the granulosa into deep folds. There is some hemorrhage at the point of rupture, but any slight hemorrhage in the follicle is confined between the theca interna and the granulosa, where there is a very thin connective-tissue layer. At this time the diameter has shrunk to 5 to 8 mm. The follicle wall protrudes slightly through the rupture point, and occasionally lymph is extruded into the cavity and walled off, producing a small cyst.

The growth of the corpus luteum begins immediately. Theca interna lobes grow into the folds and form connective-tissue strands, the blood vessels are engorged, and there is an invasion of leucocytes, mostly in the theca interna. The lipid content of the granulosa cells rapidly increases, and, to a lesser extent, that of the theca interna cells in which the granules are larger. At 3 days after heat, i.e., in the 2-day-old corpus luteum, the granulosa cells have increased from 10 μ to 15 μ in size. Mitoses are fairly common in the theca cells; eosinophils are common, but the spindle cell invasion (thecal) described by Corner in the developing corpus luteum of the pig has not been found. By the fifth day the granulosa cells increase to 20 μ, and by the

sixth arterioles have formed and mitosis has ceased in the theca cells. At 7 days the granulosa cells reach their maximum size, 25 to 30 μ, and on the next day connective tissue elements are becoming more pronounced. At 14 days the lipid increases in both granulosa and theca cells, and the granules begin to coalesce in the former, which, in a few cases, begin to show signs of degeneration. At 17 days both cell types are involved in the degenerative changes. By the twentieth day retrogression has well set in; large fat droplets are seen in the cells, and blood vessels and connective tissue are much more prominent. When the cow is in heat, the granulosa and theca cells of the old corpus luteum cannot be distinguished one from the other, and the capillaries undergo resorption.

The mature corpus luteum is either globular or oblong in shape. Its color is at first light brown to brownish yellow. Gradually it becomes less brown and by the seventh day it is old gold. At 14 days it is bright golden yellow, deepening to orange by the twentieth day. During involution it becomes brick red, and it remains as a bright streak of connective tissue for a year or more. In old cows retrogression is slower than in young ones (48).

The young corpus luteum measures about 6 to 8 mm. By 8 days it has increased to 18 to 20 mm. and when it is mature it measures 20 to 25 mm. There is no marked reduction in size until it is 20 to 30 days old (47). During pregnancy its size and weight remain almost constant, but the lipid globules increase in size and number after 5 months. Its removal at any time during pregnancy results in abortion, even when this operation is performed late in the period (49).

VULVA. During proestrum the vulva swells slightly, and this swelling becomes more pronounced during heat. Within the lips the mucosa becomes congested and is bright cherry red in color. The swelling subsides rapidly after heat has passed, and the vulva becomes wrinkled, but the congestion remains until a short while after ovulation (50).

VAGINA. The vaginal epithelium consists of two distinct regions. In the vestibule, and for a short distance above it, stratified squamous epithelium with frequent patches of lymphoid tissue is found; above that region stratified epithelium with a superficial layer of mucoid cells extends to the cervix uteri.

In the vestibular region during heat the superficial cells react more readily to acid stains, and the number of leucocytes increases. There is also congestion and edema, both of which are also pronounced during proestrum. By 2 days postestrum these changes have subsided, but the epithelial cells of

the middle layer have increased in size and number, and this increase is very marked by 8 to 11 days (47). Cornification increases from the tenth to the eighteenth day, after which desquamation sets in (51). Extravasation of erythrocytes is found in the more caudal portion of the region during and just after heat (47).

In the mucoid portion of the vagina the changes with the cycle are more clear-cut in the region 1 to 2 cm. from the cervix. The superficial layer consists of tall columnar mucus-secreting cells with many goblet cells interspersed between them. The latter are less frequent posteriorly. Below this layer are 2 to 6 layers of polyhedral cells. During proestrum the goblets are clear and free from granules; the cells do not stain with hematoxylin at this time but do with mucicarmine. The stroma is edematous. At heat the congestion and edema are more pronounced and the cells secrete mucin. The initiation of secretion proceeds down the vagina in a wave so that during the postestrous period the posterior portions of the mucoid region are active. The nuclei are compressed into the basal ends of the cells. Edema and congestion disappear rapidly after the end of heat; the epithelium decreases in height as the cells are emptied of their secretion, and the nuclei become oval. By 2 days postestrum the superficial layer takes on a serrated appearance and begins to stain with hematoxylin more intensely than it did before; the polyhedral cells increase in number, and, though there are few leucocytes, many lymphocytes invade the stratified layer. During the mid-diestrum the surface epithelium is low columnar and vacuolated, but this is succeeded by gradual growth to the next proestrum (47).

Smears from the vestibule show increased numbers of cornified cells during proestrum and estrus, but leucocytes are never absent; individual variation is so great that little reliance can be placed on the smear as a method of diagnosis. Deeper smears contain more epithelial cells and lymphocytes. There is a sudden, marked increase in leucocyte content 3 hours after mating (52). This would appear to be due not to friction but to the presence of semen in the tract, since the condition also follows artificial insemination (53).

It should be noted that the extravasation of blood in the vaginal wall is small and insufficient to color the mucus. Recent work suggests that it may occur during the proestrum and also at about the twelfth day postestrum, indicating that it happens at the periods of most intense growth in the vagina (4).

UTERUS. The cervix uteri is covered with a single layer of mucoid epi-

thelium which is much folded. The changes during the cycle are similar to those described for the upper vagina: congestion and edema during, and just after, heat; cubical cells in the diestrum, becoming columnar and full of mucin during heat, discharging and becoming ragged and cubical about 72 hours after heat (1). The epithelial cells reach their greatest height at 17 to 18 days; secretion begins at the tips of the folds, and exhaustion of the cells is not complete in the crypts until about the fourteenth day (51).

The uterus contains numerous caruncles or cotyledons which aid in the attachment of the fetal membranes. The stroma is somewhat more dense in the cotyledons; there are more blood vessels and no gland openings. The intercotyledonary area is richly supplied with glands, which are scanty before puberty but rapidly develop as sexual life begins (1).

At the end of diestrum the uterine epithelium is tall columnar and pseudostratified, and the stroma becomes congested and edematous. These changes increase during, and for a day after, heat. At the second day the congestion and edema have decreased while the cells, which have begun to secrete, are flatter. At this time, also, many of the congested blood vessels break down, and extravasated blood is present, especially in the cotyledons. At no time does the epithelium break; the erythrocytes find their way in large numbers into the lumen by diapedesis. This is the source of the postestrous bleeding. There is a similar, but much less severe, extravasation of blood at about the tenth day which does not appear as a vaginal discharge (47). This occurs at about the same time as the interheat vaginal congestion. The causes of neither of these extravasations have been worked out, and more information is needed upon the effects of different hormone levels before the condition can be understood. The glands are fairly quiescent and the lumens straight during proestrum and heat. At 2 days postestrum they are more coiled, and the lumens are filled with secretion; they begin to hypertrophy as the corpus luteum grows, and they are at their greatest growth at about 12 days postestrum. At the fifteenth day retrogression begins.

The muscle fibers of the uterus are longest at the time of heat and for 2 days afterwards. This growth begins at the tubal end of the uterine horns and spreads toward the cervix. Afterwards the fibers diminish in size and are shortest at about the seventeenth day. They have most spontaneous activity when they are longest (54).

OVIDUCT. The tubo-uterine junction of the cow is at the tip of the cornu. It is straight, without a villus, and with only a slight sphincter, which does not prevent the passage of fluid from the uterus into the tube (55).

The tubal epithelium has a distinct cycle. More mucus and leucocytes are found in the lumen at 2 days postestrum than at other times; the epithelium becomes lower at 8 days, and at this time numerous globules of cytoplasm, the centers deeply staining with hematoxylin, are found. These have been interpreted as extruded nuclei, but, to the writer, they appear to be secreted protein which is imbibing fluid at the periphery, thus staining less deeply in that region than at the center. During proestrum the cilia are much more prominent than they are earlier, and the cells enlarge. They are tallest during heat and lowest at from 8 to 12 days, when the protein has been extruded.

PHYSIOLOGY OF THE FEMALE TRACT

One of the main external characteristics of the heat period is the secretion of large quantities of stringy mucus, which is derived partly from the mucoid epithelium of the vagina and partly from the seal which plugs the cervix when the cow is not in heat. This liquefaction is brought about by a change in pH which occurs at heat. The literature on this subject has been summarized (56). *In vitro* specimens of the vaginal secretions are rarely acid. During the diestrum they average pH 8.1, dropping to 7.2 at heat, while the cervical mucus is about 1.5 units lower. The injection of estrogens into sterile cows brings about the shift in pH observed during heat (57). The *in vivo* changes are not so marked; the secretions are less alkaline, and they may even be acid (56,58).

The flow properties of the mucus have been investigated, and they may be used as an indication of physiological heat when psychological signs are slight. The viscosity is least, and the flow elasticity is greatest, at heat. The decrease in viscosity begins 24 hours before heat, and it has risen again by 60 hours postestrum (59). In the ovariectomized cow a flow of mucus can be produced by the injection of small amounts of estrogen, 350 to 1,000 R.U. daily; with larger doses, 10,000 R.U. and upwards, it is suppressed because of the cornifying action of these large doses upon the vaginal epithelium (60). During pregnancy the cervical seal is exceptionally tough in spite of the estrogens present at that time.

The motility of the uterus during the cycle has been studied by the balloon technic (61). Activity is very marked during heat and for 2 to 3 days after ovulation, but the uterus becomes relatively refractory to pituitrin immediately after ovulation. Spontaneous activity decreases until the eleventh

to the sixteenth day after ovulation, but from that time onward spontaneous activity and response to pituitrin increase, to become greatest during heat. Ovariectomy abolishes spontaneous motility. Uterine strips have been studied in detail (54). Spontaneous motility is greatest in these during proestrum and estrus, when the muscle fibers are longest; it becomes irregular during metestrum and dies down in diestrum. Two types of waves have been observed, strong contractions of great amplitude at intervals of 1.5 to 2 minutes, and small contractions at intervals of 20 to 30 seconds. The latter increase in importance during metestrum and are a large factor in the production of the irregularity. In early diestrum long rhythmic changes of tone also occur. Sympathicomimetic drugs are active at all times in the cycle, but parasympathicomimetic drugs are irregular in their action or even inert. Epinephrin is inhibitory during the estrogenic phase and motor in the lutein phase of the cycle. The cow is similar to the dog and cat in this respect. During proestrum there is a tendency for a diphasic response to appear, first a slight contraction, followed by a marked relaxation. After ovariectomy spontaneous activity is not always abolished, but epinephrin is without effect, a difference from the result found in the cat (60). If the ovariectomized cow is treated with estrogen, the characteristic spontaneous, and also the epinephrin, responses are evoked. If she is treated with 250 R.U. of estrogen and 18 Rab.U. of progesterone together each day for 6 days, a marked diphasic response to epinephrin is given. If the progesterone is increased to 35 Rab.U. daily, the estrogen relaxation with epinephrin no longer occurs and contractions result. With these doses of estrogen the low progesterone cows showed an approximation to the estrogen type of spontaneous activity; with increasing doses of progesterone the activity became less in amount and more irregular.

The level of estrogen in the follicular fluid of cows is about 321 M.U. per kg. of fluid (62) or, in ovaries at the time of heat, 4.6 R.U. per follicle (63). The minimum dose of estrogens that will bring the spayed cow into heat is 350 R.U. of estradiol benzoate for 2 days, and the average dose is 600 R.U. per day for 3 days. The less vigorous the heat period in normal life, the harder it is to bring the cow in heat after ovariectomy. Even though the injections are continued, the cow remains in heat for less than a day. The central nervous system becomes refractory, since the usual changes in the uterus and vagina continue. As this threshold is very low, it is logical to assume that in the normal cow it is reached early in the development of the follicle. As refractoriness sets in quickly, the cow goes out of heat although

the follicle is still growing. Hence the fact that the cow, alone of all known animals except the bat, in which the cause may be different, is out of heat before ovulation. Estrogens cannot be detected in the urine at any time of the cycle (60).

The corpora lutea contain from 8 to 14 Rab.U. of progesterone per kg. of fresh tissue (64). As was mentioned above, the injection of 18 Rab.U. daily for 6 days, together with 250 R.U. daily of estrogen, brings about a diphasic response of the uterine muscle to epinephrin, while an increase to 35 Rab.U. daily brings about the pure diestrous response; hence the minimal output of progesterone by the corpus luteum is probably between these figures (60). These amounts are exceptionally low for so large an animal.

The output of estrogen during pregnancy is also very low. The rate of excretion in the urine is around 200 R.U. daily for the first 100 days. It then gradually rises to about 1,000 R.U. at 200 days, after which the rise is more rapid, so that at the time of parturition the rate of excretion may be as high as 6,000 R.U., though it is usually less than 3,000 R.U. (65,66).

The anterior pituitary of cattle contains very little F.S.H., the lowest yet known (67,68). The content of L.H. is about the same as that of the hog but is considerably lower than that of the sheep. The cow seems to have a low level of sex hormone activity throughout. The freemartin, female cotwin to a bull, is usually sterile because the gonads have been modified toward the male. Probably this is due to the low threshold of the hormones involved. The cat also has the anastomosis of blood vessels regarded as necessary for the production of this anomaly, but feline freemartins have not been found. The cat has a higher level of sex hormone activity throughout, so the threshold which would produce a change may be higher and not attained during pregnancy.

The level of prolactin in the anterior pituitary is high, about 400 to 500 B.U. per gram of fresh tissue (69). This may account for the longer life of the corpus luteum of the cow, longer than is usual in mammals, though little is known of the comparative levels.

The gonadotrophic hormones are said to be concentrated in the medulla, and the lactogenic hormone in the cortex, of the pituitary (70). The content of the former falls steadily during gestation (71).

It has been reported that 1,500 I.U. of pregnant mare's serum does not produce ovulation in the presence of the corpus luteum, but that 5,000 I.U. is effective (14); another report records that 700 M.U. is the most effective dose. The follicles rupture 48 to 72 hours after injection, and the normal

to the sixteenth day after ovulation, but from that time onward spontaneous activity and response to pituitrin increase, to become greatest during heat. Ovariectomy abolishes spontaneous motility. Uterine strips have been studied in detail (54). Spontaneous motility is greatest in these during proestrum and estrus, when the muscle fibers are longest; it becomes irregular during metestrum and dies down in diestrum. Two types of waves have been observed, strong contractions of great amplitude at intervals of 1.5 to 2 minutes, and small contractions at intervals of 20 to 30 seconds. The latter increase in importance during metestrum and are a large factor in the production of the irregularity. In early diestrum long rhythmic changes of tone also occur. Sympathicomimetic drugs are active at all times in the cycle, but parasympathicomimetic drugs are irregular in their action or even inert. Epinephrin is inhibitory during the estrogenic phase and motor in the lutein phase of the cycle. The cow is similar to the dog and cat in this respect. During proestrum there is a tendency for a diphasic response to appear, first a slight contraction, followed by a marked relaxation. After ovariectomy spontaneous activity is not always abolished, but epinephrin is without effect, a difference from the result found in the cat (60). If the ovariectomized cow is treated with estrogen, the characteristic spontaneous, and also the epinephrin, responses are evoked. If she is treated with 250 R.U. of estrogen and 18 Rab.U. of progesterone together each day for 6 days, a marked diphasic response to epinephrin is given. If the progesterone is increased to 35 Rab.U. daily, the estrogen relaxation with epinephrin no longer occurs and contractions result. With these doses of estrogen the low progesterone cows showed an approximation to the estrogen type of spontaneous activity; with increasing doses of progesterone the activity became less in amount and more irregular.

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periodicity of the cycle is not disturbed. Injections were made 4 to 8 days after normal heat (72).

New ova are produced during adult life from the neogenic stratum below the ovarian tunic and not from the stratum germinativum (73). The cow's ovum has been described and measured; it is 120 μ in diameter without the zona pellucida (74). The pH of the uterus from which this specimen was obtained was 7.1, which agrees well with the pH recorded by others (53). Tables showing the rate of prenatal growth of the embryo and fetus have been prepared (75).

THE MALE

At 1 month of age the testis consists mainly of mesenchyme. Cells of Leydig are formed by 3½ months; from 2 to 5 years of age they are highly vacuolated, then the vacuoles diminish. The androgen content of the testis increases at a uniform rate during the first 2 years. From 2 to 5 years it increases sharply, and thenceforward it decreases. There are no striking changes in the Leydig cells or in the androgen content of the testis at puberty (76).

At 63 days a few primary spermatocytes may be found in the tubules, at 181 days they are abundant in all tubules, and at 224 days spermatozoa are fully formed (77). The testis increases tenfold in size from birth to 3 months and threefold from the fourth to the seventh month. Spermatozoa are formed at 6 months, and at 7 months they are free in the lumen of the tubules (78).

Spermatozoa remained potentially motile in the epididymis isolated from the testis for over 2 months (79). It is interesting to note in this connection that Aristotle was led to deny any direct reproductive function for the testis because a bull remained fertile for a while after it had been castrated (80). In the ampulla of the vas deferens spermatozoa remain motile for less than 72 hours (81).

After service the cervix of the cow is filled with spermatozoa within half an hour, the first sperm enter the uterus in less than 40 minutes, and they are at the ovarian ends of the oviducts in 4 hours. In one case the time was 1¾ hours. Motility is maintained for 30 hours; after 40 it is slight or absent, but if artificial insemination is performed outside the heat period, survival is only for 10 to 15 hours (82). The optimal conditions for survival are found in the cervix uteri, but, according to one report (19), the time of survival here is 15 hours at most. The spermatozoa do not depend entirely upon their

own powers of locomotion, since after artificial insemination of a cow with dead sperm they were found in the oviduct (82).

The normal ejaculate is an opaque, white to yellowish-white, milky or creamy fluid, and the higher the sperm content, the whiter it is. For dairy bulls the mean volume is 4.6 cc., with a modal ejaculate of 4 to 5 cc. (83). Other records give $3.7 \pm .2$ cc. (84), and 4.2 cc. (85). The mean sperm content is 1,010,800 per cu. mm., with a wide range from 120,000 to 2,144,000, and a modal frequency of 750,000 to 1,250,000 (83). These figures are very close to those given by most other workers, and they may be regarded as typical. The mean pH is $6.9 \pm .07$ (84), also typical of most results. In this case the range was 6.39 to 7.81. The same paper gives the Δ as 0.62° C. Semen is well buffered in the region of pH 4.0 to 5.5 and from pH 9.0 to 10.0, but buffering is higher on the acid than on the alkaline side of neutrality. As the curve for fluid from the seminal vesicles is very similar to that for whole semen, probably the secretion of these glands determines the shape (86).

There is no seasonal variation in pH; the semen volume is least in July to September; initial motility and power of survival are least, and the proportion of abnormal spermatozoa is greatest, also in these months. The best semen is produced in the spring (78). There is no difference in effectiveness if artificial insemination is performed with a volume of semen over a range of 0.4 to 6.0 cc. (83).

The pH of the seminal vesicle secretion, taken post mortem, varies from 5.5 to 6.5 (88). The K, Na, and Ca content of some of the secretions of the male tract are given in table 8 (89).

For range (beef) cattle the semen volume was $4.84 \pm .07$ cc., with a modal distribution from 3.5 to 5.5 cc., and 80 per cent between 2.5 and 7.5 cc. The mean concentration of spermatozoa was 1,160,000 per cu. mm., with a mode of 1.1 to 1.3 millions, and 80 per cent between 0.7 and 1.7 millions (7). These figures are a little higher than similar means for dairy bulls.

Bull's urine contains 200 M.U. of androgen per liter (90).

TABLE 8. Average Composition of Secretions from the Accessory Sex Organs of the Bull

ORGAN	CONTENT, mg. per 100 cc.		
	K	Na	Ca
Epididymis	278.4	115.0	81.7
Ampulla	320.8	165.4	26.7
Vesiculae seminales	326.1	138.5	32.6
Sperm serum	227.8	277.8	33.9

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Bos (Poephagus) grunniens L.

YAK

The yak in Russian Asia reaches puberty at the age of 24 to 30 months. The breeding season is well defined lasting from June to November, during which time the female is polyestrous. The gestation period is 258 days (1).

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Bos (Bibos) gaurus H. Smith

GAUR

In Malaya the gaur has no special breeding season, and it calves at any time of the year, though it does so infrequently from October to December, the wettest months (1). As the period of gestation is 9 months, mating must be relatively infrequent during the period of January to March. In India it breeds at different seasons in different districts, but the most frequent breeding time is in December and January, and births are mostly in August and September. One or two are born (2), though twins are said to be rare (1).

The evidence suggests a polyestrous animal, and this is supported by the fact that *B. frontalis* Lambert, the gayal, which is the domesticated form of the gaur, has a 3-week cycle all the year round (3).

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Bos (Bibos) indicus L.

ZEBU, HUMPED CATTLE

The cycle of the zebu is essentially similar to that of European domestic cattle. The mean cycle length is $23.03 \pm .19$ days, and the standard deviation is 6.64 days. The modal length is 22 days. The mean length of heat is $4.78 \pm .07$ hours, with a standard deviation of 2.20 hours, and a modal length from 3.5 to 5.5 hours. The exposure of these cattle to an additional length of daylight (in Kenya) had no effect upon the duration of heat (1). This length of heat suggests that the zebu has a lower sex hormone circulation even than the cow. Comparison of the F.S.H. content of the anterior pituitary with that of the cow would be interesting. The external signs of heat are practically unrecognizable, and vasectomized bulls have to be used to work out the length of the heat period (2).

The estrogen excretion during pregnancy is as follows (3):

At 93 days,	33 M.U. per liter
101–150 days,	443 M.U. per liter
151–200 days,	555 M.U. per liter
201–250 days,	833 M.U. per liter
251–term	1,100 M.U. per liter

The sex ratio of 8,770 calves was $50.92 \pm .36$ per cent males (4). The duration of gestation is about 285 days (5).

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Bos (Bison) bison L.

BISON, AMERICAN BUFFALO

The bison in captivity has estrous cycles of about 3 weeks' duration all through the year (1), but records of the numerous herds when they were at large on the North American prairies indicate that in a state of nature their main mating season was from July to September. The period of gestation is about 9 months (2). In Canada the breeding season is restricted, beginning toward the end of July and lasting for 6 weeks. The duration of heat is believed to be fairly long, at least 2 days (3).

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Bos (Bubalus) bubalis L.

EURASIAN BUFFALO

The buffalo reaches puberty usually at 2 to 3 years of age, but it may do so at 1.5 years with good feeding (1). The cycle recurs at intervals of about 3 weeks all the year round, but its length is more variable than is that of the cow. One series of figures gives an average of 21 days, with 6 cases between 13 and 16 days, 26 between 17 and 23 days, and 12 between 24 and 28 days (2). In the Chinese buffalo the cycle is said to recur every 28 to 30 days, and the same is reported for the Indian buffalo (3). The Bulgarian buffalo is said to have heats at 3-week intervals, and heat lasts from 24 to 36 hours, rarely 48 hours (4). The heat period in the Philippine carabao and in the Indian buffalo lasts less than 1 day (5). In the Malayan water buffalo heat is said to recur at monthly intervals and to last for 2 weeks if fertilization does not occur (6). This, if true, is an unusual type of behavior for Bovidae.

The Asiatic buffalo has been divided into two races, a swamp race without a neck to the scrotum, with nocturnal mating, and with the first heat follow-

ing parturition at about 65 days. The other, the river race, has a pendulous scrotum, daytime mating, and a "calf" heat at about 42 days (7). In Bulgaria the average "calf" heat occurs 118 days after calving (4), and in the Philippines the carabao has an interval of 34, range of 24 to 50, days. The Indian buffalo in the same region has an interval of 49, range of 45 to 53, days (5).

In Italy primiparae are said to bear their young mainly in March and April, and the multiparae in August and September (8). In the Philippines most cows calve from September to January (5). One or two young may be born at a time. The period of gestation is variously given and it may vary with the race, as it does with domestic cattle. The means given in table 9 vary from 305 to 332 days. One wonders whether these diverse records of breeding behavior all refer to one species.

TABLE 9. Gestation Periods of Buffalo

RACE	GESTATION PERIOD, DAYS	
Transcaucasian (1)	305	
Italian (8)	311 ± .08	Range, 287–337
Chinese Water (9)	312	
Surti (10)	312.7	Range, 299–325
Indian (6)	315	
Bulgarian (4)	315	Range, 302–328
European (2)	315	Range, 303–326, n = 94
Carabao (5)	316.2	
Asiatic River (7)	317	
Philippine Carabao (11)	322	Range, 318–328
Macedonian (12)	325	Range, 320–330
Asiatic Swamp (7)	332	

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Bos (Syncerus) caffer Sparrman

AFRICAN BUFFALO

The evidence regarding the breeding season of the African buffalo is somewhat conflicting, suggesting a fairly prolonged season, the length of which depends upon climatic conditions. In South Africa the breeding season appears to be from September to March, the spring and summer, and as the gestation period is about 11 months, the calving season is about the same (1).

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CAPRINAE

Ovis aries L.

DOMESTIC SHEEP

The domestic sheep is polyestrous, with cycles recurring at about 16.5-day intervals. Fine-wooled breeds tend to be polyestrous all the year round, a result, perhaps, of the fact that they have been developed in warm conditions without extreme seasonal climatic changes. The coarse-wooled breeds are seasonally polyestrous, with their season beginning about September in the Northern Hemisphere and continuing, in the absence of pregnancy, well into winter. In the Southern Hemisphere the breeding season begins at the corresponding time of the year, i.e., about March. Sheep transferred from one hemisphere to the other rapidly adjust themselves to the changed seasons. Ovulation is spontaneous, occurring toward the end of heat. The corpus luteum is active for about 14 days, and proestrum is ill defined. Uterine changes during the cycle are not well marked, but the vaginal smear is a fair indication of the reproductive state. The pituitary of the sheep has a moderate F.S.H. content, and the L.H. level is fairly high. The period of gestation is about 150 days; the number of lambs varies from 1 to 3, depending largely upon the breed. The ram produces spermatozoa all the year round, but there is a tendency toward quiescence during the summer months in

the coarse-wooled breeds. The chief practical problem in sheep breeding is to lengthen the season and to produce ovulation and pregnancy during the anestrum.

THE ESTROUS CYCLE

Merinos, Central European (1), Karakul (2), and Persian Blackhead (3) sheep tend to breed all the year round, but the presence or absence of an anestrous season during the summer depends largely upon climatic and feed conditions. Thus, in some regions of South Africa, Merinos have a definite breeding season from February to August (3). In the Tzurcana breed of Rumania there is a short anestrum in July (4), and in the Romanov breed of Russia ovulation often occurs in summer without external signs of heat (5). This is not the rule, however; usually during anestrum the ovaries are quiescent. The Dorset Horn also has a prolonged breeding season. In India the Bikaner ewe will breed at any time of the year, but two seasons predominate in lambings, spring and autumn (6).

The coarse-wool breeds generally begin to come in heat about September 1, and, if not bred, they continue to have cycles until about January 1, on the average, though many individuals continue even until May (7). There are breed differences in the incidence of the season: Rambouillets tend to come in heat earliest, followed by Hampshires, Southdowns, Shropshires, and Romneys in that order (8,7). Lambs usually begin to breed during their first season, at a mean age of 213 days and a range of 187 to 250 days, but late-born lambs wait until the next season for their first heat period (7). The first heat period of lambs during the season is usually later than that of mature ewes (8). In Merino ewes with a season limited by climatic conditions the onset of the season is gradual, with several weak estrous periods without ovulation before the true breeding season sets in (9).

The duration of the cycles is remarkably constant, but the Merinos and Rambouillet cycles are about a day longer than those recorded for other breeds. A series of recorded means is given in table 10. The mean length of succeeding cycles is variable and does not seem to follow any definite pattern (10). No heat occurs in Merino sheep during lactation, but, if the lambs are weaned immediately after parturition, it usually follows in 60 to 150 days.

The mean length of the heat period for Scottish sheep is 36 hours, with a mode of 28 hours and a range from 3 to 84 hours (11). For Merinos it is slightly longer (7), with a mode from 36 to 48 hours (70 per cent of cases)

(18); in South Africa the mean is 30 hours and the mode, 30 to 32 hours (3), but in Australia 50 per cent of Merinos are said to be in heat for less than 19 hours (15). Records for mixtures of breeds, mainly coarse-wool, give 30 to 40 hours, but rarely less than 24 hours or more than 48 hours (8), with a mean of 29.3 hours and mode of 21 to 27 hours (7). It may be concluded that the mean heat period is from 30 to 36 hours, with but little difference between breeds. Service has no effect upon the length, and long heat periods

TABLE 10. Length of the Estrous Cycle in Sheep

BREED	LENGTH OF CYCLE, DAYS	RANGE, DAYS	REMARKS
Scottish (11)	16.4 ± .8	15–18.5	Mode, 16.5
Navaho (12)	16.44 ± .10		
Hampshire (10)	16.5		Flushed
Shropshire and Hampshire (7)	16.7		Mode, 17; 68 per cent from 15.5–17.5
Romney (13)	16.7		Mode, 17; 89 per cent from 14–19
Merino (3)	16.8	12.5–18.5	Mode, 16.5
Tzigai (14)	17	16–21	
Dorset (15)	17		
Merino (15)	17		
Romney (16)	17.0	14–39	91 per cent from 15–18
Hampshire (10)	17.2		Unflushed
Merino (17)	17.3		Mode, 17. Grades
Merino (18)	17.4 ± .08	6–27	Mode, 17; S.D., 1.8; 85 per cent from 16–19
Rambouillet (10)	17.5	13–21	
Tzurcana (4)	17.5	15–20	

are usually more intense than short ones (11). However, a slight shortening after sterile service has been reported (7). Ovulation without heat occurs frequently at the beginning and the end of the breeding season, and there is no correlation between the length of heat and the length of the cycle (7).

Ovulation usually occurs from 18 to 24 hours from the beginning of heat, or from 12 to 24 hours before its end (11); at from 23 to 30 hours from its beginning (7); or, according to another report, in Merinos, at from 36 to 40 hours from the beginning, with heat finishing 6 hours after rupture of the follicle (18). The time of ovulation is more closely related to the end of heat than to the beginning, i.e., ovulation tends to cause its termination.

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It may occur as early as 11 hours before its end, or as late as 6 hours afterwards, but, in general, it is before the end. In the case of twin ovulations, 1½ to 7½ hours may intervene between the two, with a mean of 1¾ hours (7). However, Merino and native Masai sheep in East Africa are said to ovulate shortly after the end of heat (19). The exact time of ovulation in relation to the end of heat is difficult to obtain as it can only be determined by laparotomy, which, in itself, may interfere somewhat with the length of the period or with its determination. The right ovary functions more frequently than the left, since ovulations have been found in that ovary in 57 per cent of cases (7), or 52 per cent (20), or 58.58 ± 1.85 per cent (21).

The onset of heat is usually abrupt, but the cessation is gradual. Heat does not begin more frequently during the day or night (7), though one record (15) found a slight tendency for it to begin more often during the hours of daylight. There are breed differences in the intensity of heat; Dorsets are easier to detect than Merinos as there is more swelling and reddening of the vulva in the former. Moreover, the Dorset has a characteristic stance whereas the Merino tends to be more restless. Ewes attract the rams before they will accept coitus. Apparently the latter are attracted to the ewes by the olfactory sense as vaginal and perineal swabs from ewes in heat, when applied to pregnant ewes, make them attractive to the rams (15).

The time of mating or of artificial insemination within the heat period is not as important as it is in most other species. In one experiment with Kazac ewes service at 8 hours from the onset of heat resulted in 70 per cent conceptions, from 16 to 32 hours it varied from 82.5 to 86 per cent, from 40 to 48 hours it was 77 per cent, and at 56 hours it was 67 per cent. The onset of heat was detected by vaginal smears, a method which places this time rather earlier than does a test by the ram (22). Another experiment gave similar results (23). The optimum time of artificial insemination is said to be 18 to 26 hours after the onset of heat (24).

The rate of travel of ova through the oviduct is similar to that in other species. They are all in the middle third of the oviduct by 5 hours after heat has ceased. At 60 hours most are still in the middle third, but a few have reached the last third or even the uterus. By 72 hours most are in the uterus (15).

In those breeds which experience heat all the year round it is theoretically possible for the ewe to have two lambings a year. This is recorded, for instance, for the Wryosowka breed (25). The number of lambs produced at a lambing is very variable; 1 to 3 is the rule, but quadruplets are not in-

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frequent in some breeds. Fecundity is a breed characteristic, and there are very wide differences between breeds. The most recent data are summarized in table 11. It may be noted that the hill breeds are the less fecund, while the lowland breeds, especially those which are kept for their milk, are the most fecund. It is generally agreed that fecundity is relatively low at first, rising to a peak at about the sixth year. The usual practice is to breed ewes at their second season, but most will breed as lambs in their first year, though it seems to affect their subsequent fecundity adversely. Table 12 illustrates this fact for Hampshire ewes and also shows the rise in fecundity with the age of the ewe (26). Both the tables dealing with the fecundity of ewes consider only those which conceive; they do not take into account the incidence of sterility. The percentage of multiple births tends to be highest in ewes bred early in the season. It may be stated as a general principle that ease of reproduction, fecundity, and the length of life during which reproduction is possible are related, and the sheep is no exception to this rule. An animal's early performance is a good index of its lifetime capacity, provided that its readiness to breed is not abused. The variation of fecundity with the breed implies that it is an hereditary factor; not only is this so between breeds, but it holds true within a breed. For Romanov sheep this is well illustrated by table 13 (27), which gives the numbers of lambs born to ewes which were, themselves, singlets, twins, etc. In the Dorset breed there is a tendency for more multiple births in the spring than in the fall (28), which suggests that reproduction is more intense at the normal breeding season for the species than it is at other times.

Data on the sex ratio show great constancy. In general, analysis of farmers' records gives a ratio of 49 to 50 per cent males, but records from experiment station flocks have often given a slight preponderance of males. The fetal sex ratio is a little higher, averaging 50.9 ± 1.60 per cent males, with no significant difference with the age of the fetus (21). The ratio for stillbirths is 53.8 ± 2.9 per cent males (29). These figures suggest that the sex ratio at or near conception is not so markedly different from the secondary ratio as it is in the pig and in man. The ratio does not alter when singles, twins, and triplets are considered separately, but there is an excess of twins of opposite sex, which indicates that there is little or no monozygotic twinning in sheep (29).

Some mean durations of gestation are given in table 14. In general, the early maturing meat breeds have the shorter gestations. An analysis of periods from Rambouillet ewes gave a range from 143 to 159 days, with a standard

TABLE 11. Fecundity in Sheep

BREED	LAMB CROP, PER CENT
Cheviot (30)	89.1 ± 1.69
Scottish Blackface (30)	93.1 ± .85
Heath (31)	102.7
Karakul (32)	110
Corriedale, in Canada (33)	114.0
Corriedale, in U.S. (34)	118
Southdown (35)	119.3 ± 1.9
Rambouillet, in U.S. (34)	122
Rambouillet, in Canada (33)	124.0
American Shropshire (28)	124.4
American Shropshire (36)	126.2
Oxford Down (37)	126.9
Columbia (34)	127
Dorset (28)	127.4
Romney Marsh (37)	128.5
Navaho (12)	128.6
Targhee (34)	129
Hampshire Down (37)	131.8
Dorset Horn (37)	136.9
Lincoln (37)	138.9
Suffolk (37)	144.3
Canadian Corriedale (33)	146.0
Shropshire (37)	162.0
Leicester (37)	163.0
Wensleydale (38)	172
Border Leicester (37)	181.0
East Friesian Milch Sheep (39)	205.1
Romanov (40)	238

TABLE 12. Fecundity of Hampshire Ewes

	BRED AND CONCEIVED AS LAMBS	BRED AND CONCEIVED AS 1½-YEAR-OLDS
	Lamb crop, per cent	*Lamb crop, per cent*
First season	106	—
Second season	157	195
Third season	176	202
Fourth season	177	175
Fifth season	200	208

TABLE 13. Effect of the Number Born on the Subsequent Fecundity of Romanov Sheep

EWES BORN AS	AVERAGE LAMBS PRODUCED BY THEM
Singles	2.17
Twins	2.36
Triplets	2.63
Quadruplets	3.01

deviation of 2.25 days, which agrees closely with that for other breeds (41). In this series there was a tendency for ewes bred early to have slightly longer periods than those bred late, and the period lengthened with age. Eight-year-old ewes had an average gestation period nearly 2 days longer than 2- and 3-year-olds. A gestation resulting in a single birth was about 0.6 of a day longer than that resulting in a twin birth. The sex of the lambs born had no effect on the duration (42).

HISTOLOGY OF THE FEMALE TRACT

OVARY. While considerable work has been done upon the development of the follicles and corpora lutea during the breeding season, information on the development of the ovaries in lambs appears to be lacking. During anestrum the ovaries are quiescent. Toward the end of this period waves of follicles grow, but they become atretic before they mature, and no new corpora lutea are formed, while those from the previous season have disappeared. In proestrum it is easy to distinguish the follicles which are destined to rupture later unless large atretic follicles are present. Growth is rapid during heat, all the layers of the follicle become thin, vascularity increases, and the cumulus becomes dome-shaped and large. At the time of ovulation the follicle is about 1 cm. in diameter (8). A few hours before ovulation the follicle swells beyond the surface of the ovary, becoming conical. One hour before rupture a small round area becomes clear and transparent; a few minutes before rupture a cone, occasionally more than one, appears. This breaks, follicular fluid flows out, and the follicle gradually collapses. The fluid rarely spurts; at first it is thin, but it becomes viscous within 2 to 3 minutes (7). The follicle opens with ragged borders; a small blood clot closes the opening, though not unless a blood vessel is involved in the rupture area (7); but there is no hemorrhage into the cavity. The

TABLE 14. Duration of Gestation in Sheep

BREED	DURATION OF GESTATION, DAYS
Dorset Horn (43)	144.1
Hampshire (41)	145.0 ± .02
Shropshire (41)	145.6 ± .08
Columbia (42)	148.0
Heath (44)	148.1
Merino (44)	148.5
Rambouillet, bred to Hampshire ram (45)	148.6
Merino, flesh (41)	149.0 ± .08
Tzigai (14)	149
Navaho (12)	149.4
Corriedale (42)	149.5
Targhee (42)	149.5
Ronderib-Afrikaner (46)	149.6
Rambouillet (45)	150.5
Rhon (41)	150.8 ± .1
Rambouillet (42)	151.0
Merino, wool (41)	151.2 ± .07
Karakul (47)	151.8 ± 1.60

follicle walls grow in, and the cavity is completely filled by 30 hours after ovulation. The corpus luteum reaches its maximum size at about 6 to 8 days, and it is then about 9 mm. in diameter. It has lost its rupture point. At first it is reddish pink, becoming paler up to the next proestrum, when a yellowish tinge appears as fatty degeneration sets in (18). After this, degeneration is rapid, so that by the time it is 24 days old only vestiges remain. The corpus luteum of pregnancy remains until parturition (8), though atrophy begins about 2 to 3 weeks before (11).

The corpus luteum is developed from both granulosa and theca interna cells, but the lutein cells almost all have a granulosa origin as the theca lutein cells quickly degenerate. The lutein cells measure 25 to 30 μ at first, and they gradually increase in size until retrogression sets in at the fourteenth day (48). The size of the ovum is 147 μ, and the zona pellucida measures 15 μ (49). The ovarian tunic is a tough structure. No new ova are produced during sexual life from the germinal epithelium, but the neogenic layer below the tunica albuginea does produce them. The first polar body is usually extruded from the ovum just prior to or, in many cases, just after ovulation (8).

VAGINA. The vagina does not undergo striking changes during the

cycle. Except in anestrum there is continuous growth of the epithelium, slightly accelerated during heat; late in the heat period and in metestrum considerable desquamation occurs, often as many as 4 to 5 layers of cells being cast off. Partial keratinization is characteristic of the heat period, but it may occur at any time; it is always regional and never general. Lymphocytes and leucocytes may be found in the epithelium at any time, but the latter are most frequent early in diestrum (11). These cells are present in greatest numbers at about the seventh to eighth day after ovulation (7,8). The vaginal stroma is most edematous in late proestrum and early in heat. During the first 10 days of diestrum most mitoses are found in the epithelium, and at this time the cells are most reactive to basic stains. Their greatest affinity for acid stains is shown at proestrum and on the first day of heat (50).

Some workers have found the smear to be more clear-cut than the changes in the vaginal epithelium would lead one to expect. During late proestrum and early heat the smear contains epithelial cells, leucocytes, and scant, thick mucus; the latter does not appear in diestrum. This stage lasts about 12 hours. Then the mucus becomes voluminous and transparent, with small epithelial cells, very often a few squamous cells, and usually leucocytes. This stage begins at about the fourth hour of heat and lasts for about 24 hours. On the second day of heat the leucocytes are reduced in numbers. This stage lasts through the first day of metestrum. On the second day desquamation increases, and the smear becomes voluminous, dry, and cheesy. It consists mostly of large squamous cells, with occasionally a few leucocytes, and it lasts for about 4 to 8 days. In late diestrum the number of small epithelial cells and leucocytes increases; the smear is still voluminous but is moist (8). Some workers, however, have found the smears much less distinct. The changes are said not to be characteristic of the stage of the cycle in the Karakul (51) and the Tzurcana (4) breeds, though in the latter cornified cells are absent during anestrum.

The ewe does not secrete the large quantities of mucin which are characteristic of the cow, probably because of the higher level of estrogen, but some is secreted from the glands of the cervix, not from the vaginal epithelium. Mucin builds up in the cells during diestrum and is greatest in amount late in this period. It is secreted in proestrum and early heat, becoming more fluid during heat (7). The glands are less complex in anestrum than at other times (8).

UTERUS. The chief characteristic of the uterine epithelium is the presence

of black pigment in many ewes. This is present at all times and is melanoblastic in origin and not derived from blood pigment. The cell changes during the cycle are slight. There is considerable edema and increased vascularity in both the cotyledonary and intercotyledonary areas during heat and metestrum; the glands become more coiled, and their cells increase in height with the growth of the corpus luteum. The epithelium is folded most at the mid-luteal stage. Leucocytes are found at all stages, but mostly when the corpus luteum begins to retrogress (7). In anestrum the glands become scanty and small, with low columnar cells (8).

In the cotyledonary areas the stroma is more densely cellular and more vascular than it is elsewhere. The cells are low columnar just after heat, but they rapidly grow from 11 to 17 μ to 39 to 53 μ in about 5 to 6 days. At their maximum height they tend to be pseudostratified. They retrogress rapidly after this stage, which is of short duration (50).

OVIDUCT. Changes in the oviduct are more definite than in any other part of the tract. The columnar ciliated epithelium of the branched folds in the mid-tubal area is highest in early diestrum, and the cilia are longest, while connective tissue is relatively abundant. Cytoplasmic extrusions are most apparent toward the end of diestrum. Changes at the fimbriated end precede those at mid-tube by a short time (50). During heat the ovaries are closely invested by the infundibulum (18).

The tubo-uterine junction contains no villi or sphincter, but the muscle is thickened at this point. Fluid passes easily from the uterus into the oviduct (52).

PITUITARY. Changes in the histology of the anterior pituitary in relation to the cycle have been investigated. It was found to be difficult to employ the usual acidophil-basophil classification as the differences are not clear-cut. Several cell types have been described, and they seem to vary somewhat in relative numbers during the cycle, but the clearest changes are found in the degree of granulation. This increases gradually late in diestrum, is at a maximum at the beginning of heat, and rapidly decreases during heat (53).

An increase in the number of dark-staining, usually fuchsinophil, cells during heat has been described as taking place in the adrenal cortex (54).

THE PHYSIOLOGY OF THE FEMALE TRACT

The mean vaginal pH on the first day of heat is 6.65, with a range from 5.85 to 7.40. During mid-diestrum it is 6.69, with a range from 6.00 to 7.60.

This is considerably more acid than the vagina of the cow, and the shift in the acid direction at the time of heat is much smaller (55). Perhaps it is correlated with the smaller amount of mucus secreted by the ewe.

The pH of the uterine secretions in a ewe in heat averages 7.50, and in diestrum it is 7.21 (56). The shift is in the reverse direction to that in the vagina. The motility of the uterine muscle has been investigated by the introduction of a balloon through a fistula. Spontaneous contractions of longitudinal muscle begin 1 to 2 days before heat. They reach their maximum amplitude during heat and cease after ovulation, to be replaced by segmental contractions of the circular muscle. By the fourth or fifth day of diestrum the uterus is quiescent. Contractions during heat occur at about 40 to 60 second intervals, and they become more widely spaced in early diestrum. The cervix uteri is open during heat and for a short time afterwards (57).

The injection of 1,000 R.U. of estradiol brings spayed ewes in heat, and if the dose is continued, it produces the characteristic histological changes of heat. If it is followed by progesterone, the usual changes in the uterine glands found in the lutein phase of the cycle are obtained. Estrogen increases the height of the cervical epithelium, and this height is maintained with progesterone (58). The optimal dose to bring anestrous ewes into heat is 900 to 1,500 R.U. of estrogen in divided doses (7), but there may be great variation as another report gives 3,000 R.U. as the average effective dose, with occasional records as low as 400 R.U. (8).

Ovariectomy of pregnant ewes after the fifty-fifth day of gestation is not necessarily followed by resorption of the embryos or by abortion. The chances that the pregnancy will go on to term appear to increase the later the operation is performed (59).

As the problem of extending the breeding season of the ewe is an important one in agricultural practice, a great many attempts have been made to achieve this object with gonad-stimulating hormones, but with varying degrees of success. It is very difficult to assess the value of most of this work as different breeds have been used, some with extended breeding seasons; and it has been done at different times of the year, often without any indication of the length of the normal breeding season in that particular year. Also, a great variety of extracts has been used, containing mixtures of hormones. The impression gained from the work as a whole is that it is more difficult to cause a ewe to ovulate early in anestrum than it is later, when the ovaries are undergoing some cyclical changes, not yet sufficient to bring about ovulation. If some attention were paid to the size of the follicles

present when injections are made, a clue might be obtained as to the cause of the erratic results found.

The pituitary of the ewe appears to have the same potency in terms of rat units and rabbit ovulating units at all times. It is therefore reasonable to conclude that the cyclical changes in the ovary are determined by the release of hormones from the pituitary and not by the latter's hormone content. During anestrum 50 R.U. of pregnant mares' serum is the borderline dose for the induction of heat, but 100 R.U. produce much more consistent results. Two doses of this amount at an interval of 16 days are needed, and estrus occurs after the second injection (8). Usually 250 R.U. injected twice at an interval of 16 days is recommended; it is ineffective if the interval is 14 days (60). In this work no evidence of superovulation was found when the dose given was as high as 4,500 R.U. Such evidence has, however, been obtained by the use of an unspecified amount of F.S.H. in a pituitary extract digested with trypsin to destroy the L.H. The number of eggs recovered was much less than the number of corpora lutea found, and it was believed that most of them were entrapped in the developing corpora lutea (61). A clue to the erratic nature of the responses, particularly to the difficulty in obtaining conceptions, may be found in some work which shows that horse pituitary extract (very rich in F.S.H.) and P.M.S. evoke sexual receptivity only in animals having a regressing corpus luteum. In the absence of a corpus luteum ovulation occurs without heat; the presence of an active corpus luteum usually suppresses both ovulation and heat (62). In this work it was also found that the injection of 0.5 to 1.0 mg. of estradiol benzoate or of stilbestrol dipropionate induced ovulation, probably by stimulation of the animal's own pituitary. Superovulation was obtained with horse pituitary extract when it was given in mid-diestrum. However, the dosage may be as important as the condition of the ovary since the injection of 100 R.U. of P.M.S. into anestrous ewes induced ovulation without heat, while the injection of 1,000 R.U. induced heat (63).

There is considerable evidence that the use of gonad-stimulating hormones about 2 days before the onset of a normal heat increases the number of multiple births, for instance, in Karakuls (64), and it may also increase the number of conceptions toward the beginning of the season (65).

The pituitary of the sheep is about five times as rich in F.S.H. as is that of the cow, but even so the ewe stands low in the list of animals which have been tested (66). In L.H. content the pituitary is about ten times as potent as that of the cow (67).

Tables showing the prenatal growth of the embryo and fetus have been published (68,69).

THE MALE

One characteristic of the reproductive tract of the ram is the presence of the filiform appendage, a process on the left side of the tip of the penis. This is perforated, and the tube is continuous with the urethra. Formerly it was believed that the appendage was instrumental in depositing the semen within the cervix uteri, but this is probably not so since its removal has no effect upon the fertility of the ram (70).

Primary spermatocytes make their first appearance in the testis at about 63 days of age; at 126 days secondary spermatocytes appear, and at 147 days spermatozoa are present (71). In some breeds, e.g., the Shropshires, there is little seasonal variation in mating desire, but in others there is a strong seasonal tendency. In Hampshires it is highest from October to April. In Shropshires spermatogenesis is low in summer, but it is maintained in Hampshires (72). There is evidence that in summer spermatogenesis suffers in those breeds in which the scrotum is covered with wool, thus decreasing the heat loss. Usually the scrotal temperature is 5° C. below the rectal temperature. Insulation of the scrotum for as few as 4 days increases the percentage of abnormal spermatozoa (73). In Australia it has been found that exposure of rams to 4 weeks of sustained daily maximal temperatures of 90° F., and over, causes marked abnormalities of the spermatozoa, and spermatogenesis may cease completely (74). Much of the temperature control of the testis is produced by the dartos muscle of the scrotum, which relaxes in warm weather. Isolated strips of this muscle have little or no spontaneous rhythm, but temperature variations provide the stimulus. It relaxes with an increase of the temperature and shows rhythmic activity at low temperatures. It is also responsive to sympathetic and parasympathetic drugs (73).

The epididymis of the ram is about 40 to 60 metres long when its coils are unraveled (75). It contains (average of 2 rams) 162×10^9 spermatozoa, of which 76 per cent are in the cauda. It took a mean number of 30.2 ejaculations to exhaust the rams, and by that time 84 per cent of the spermatozoa had been ejaculated from the cauda (76). Normally it takes an average of 8.8 days for the spermatozoa to travel through the epididymis (73).

During coitus the semen is deposited in the cranial end of the vagina. It is in the body of the uterus in 15 minutes and has reached the top of the

oviducts in 6 hours. The cervical canal appears to act as a reservoir for the spermatozoa (77). They can live in the vulva for 3 hours and in the vagina for 6 hours (78). It has also been reported that they may live for 12 hours in the vagina but that few survive for 24 hours. In the cervix they may survive for 48 hours, but in the oviducts they probably live for only 9 hours. In general, their motility is reduced after a stay of 12 hours in the female tract, and none survive for more than 48 hours (77). Their speed of ascent varies little whether the ewe is in heat or not (79), but it has also been stated that the oviduct becomes pervious to spermatozoa only about 15 to 17 hours before ovulation (80). The rate of travel of spermatozoa is said to average 1.26 mm. per minute in the female tract (15) or 4.6 mm. per minute *in vitro* (81).

The ovum is said probably to have a fertile life of less than 24 hours (79).

Semen may be collected in an artificial vagina, or the ram may be caused to ejaculate with an electric shock through the lumbar portion of the spinal cord. The average volume, etc., of the ejaculate collected by the two methods are given in table 15 (82). The buffering capacity of the semen is fairly high, and it is comparable to that of the bull (83). Limited analyses of certain secretions of the male tract have been made and are reported in table 16 (84). The figures are considerably lower than corresponding ones for the bull.

It has been reported that by the implantation of tablets of diethylstilbestrol into connective tissue the production of spermatozoa can be increased, but that the effect lasts only for about 5 days. It is not clear whether this represents a temporary increase in spermatogenesis or whether passage through the epididymis is hastened (85).

TABLE 15. Rams' Semen Collected by Different Methods

	SEMEN COLLECTED BY	
	artificial vagina *	electrical ejaculation
Mean volume, cc.	1.18 ± .14	1.46 ± .06
Spermatozoa, thousands per cu. mm.	1,537 ± 41	937 ± 35
Spermatozoa per ejaculate, millions	1,875 ± 110	1,354 ± 102
Mean pH	6.3	6.8

* These figures are fairly typical for rams' semen, though the sperm count is a little low.

The inheritance and growth of horns is complicated and is, to a certain extent, apparently under the influence of sex hormones. In some breeds, for

example, the Dorset Horn, both sexes are horned, though the ewe has smaller horns than the ram. In Merinos and Rambouillets the ram is usually horned and the ewe not, though she has prominences often capped by scurs at the usual points of growth. In the Suffolks, Southdowns, and other breeds both ram and ewe are hornless, and the usual growth points are represented by

TABLE 16. Composition of Rams' Semen

	K mg. per cent	Na mg. per cent	Ca mg. per cent
Epididymal secretion	165.9	87.5	18.3
Sperm serum	87.3	143.6	18.1

depressions in the skull. Crosses between horned and hornless breeds and studies of inheritance in the Rambouillet breed have shown that horns develop in the ram if he is either homozygous or heterozygous for horns, but in the ewe only if she is homozygous, though in the latter the picture is frequently obscured by the growth of loose scurs (86). Another interpretation is that inhibiting factors with a sex-limited expression may account for the results obtained on crossing (87).

In breeds which are horned in both sexes, removal of the gonads does not interrupt horn growth, except that in the wether they resemble those of the ewe and do not become as heavy or as coiled as they do in the ram. In a breed such as the Herdwick, horned in the ram and not in the ewe, horn growth ceases when the ram lamb is castrated, but ovariectomy has no effect; the ewes continue to be hornless (88,89). A similar result has been recorded for the Merino (90). It is evident that there is an interplay between hormones and genes the exact nature of which is still obscure. It would be worth while to observe the effects of the implantation of tablets of gonadic hormones in gonadectomized sheep of known genetic make-up.

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Ovis ammon L.
(= *O. poli* Blyth)

ARGALI, ARKAR

The arkar has one breeding season a year, from the end of October to December in Siberia, and the period of gestation lasts 5 months (1). Lambing is usually in early April, and the young ewes have 1 lamb while the older ones usually bear 2 (2). Older reports suggest that the arkar is monestrous and that the time of lambing varies considerably with the climate of the habitat, being later in the severer parts of the Himalayas (3).

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Ovis canadensis Shaw

BIGHORN

Puberty is usually reached at 2½ to 3 years of age. The breeding season is from mid-November to mid-December. One lamb is usually born, and the period of gestation is about 180 days (1). In the southern part of its range, e.g., in Texas, rut appears to be a little earlier as the lambs are dropped from March to April (2).

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Capra hircus L.

DOMESTIC GOAT

The goat is a seasonally polyestrous animal with a breeding season beginning about September, reaching its greatest intensity in October, and then gradually tapering off so that few goats, if held over, will come in heat in the New Year. The length of the breeding season is a matter of considerable practical importance, as it is difficult to arrange breedings so that a herd will give a uniform yield of milk all the year round. The lengths of the cycle and of heat periods are a little longer than those of the sheep. Ovulation is spontaneous. Much less work has been done upon the histological changes in the genitalia of the goat during the estrous cycle than in those of any other domestic animal, in spite of the goat's convenience as an experimental subject.

THE ESTROUS CYCLE

The length of the estrous cycle is somewhat variable, and it is generally given as about 21 days. A series of accurate determinations which were made upon the Angora goat gives a mean cycle length of $19.4 \pm .5$ days, with a spread from 12 to 24 days. The same work reports a duration of heat of 39.2 ± 1.9 hours, with a spread from 1 to 4 days (1). For dairy goats a comparable series gave a mean cycle length of $17.8 \pm .36$ days, with a standard deviation of 5.76 days (2). This data, however, is peculiar in that there are a number of cycles of extremely short duration, from 6 to 12 days. There was a very strong mode at 20 days, and 72 per cent of the observations fell between 15 and 24 days; hence the normal duration may be regarded as 20 days. The number of aberrant cycles was greater in the kids than among mature does.

A study of the frequency of kiddings in the United States, month by month, has shown that the greatest number of conceptions occur in October and that fairly good breeding may be expected from August through January; in all other months very few conceptions occur (2). A similar, more extensive, study of American records gave the most intense breeding from mid-September to mid-November and the lowest in May (3). English records give the same results, but after a cool summer the peak of reproduction

comes a month earlier, and after a hot summer, a month later, than usual (4). However, the shifts may be due to little and much sunlight rather than to the mean temperature, as it has been shown that the season may be modified by exposure of the goat to varied daylight periods. In India the Jumna Pari goat mates most frequently from July to October, but the Bar Bari goat, a dwarf type, will breed at any time of the year (5). Apparently the breeding season in that country is not so well defined as it is in temperate climates, since it is stated that 2 kiddings may occur in a year (6). The same remarks may apply to the Philippine Islands, as the mean interval between parturition and heat is 91.5 ± 8.0 days. Apparently goats in that country do not breed at so early an age as they do in temperate climates, since the mean age at first heat is given as 494 days (7). In the northern countries goats will breed as kids if they have been born early in the season.

The usual number of young born at a kidding is 2, but 1 to 3 are common, and 4 and 5 are rare. Limited data, given in table 17, indicate that some breed differences exist. The number of kids born to does below 18 months of age average 1.5, but to does above this age the average is 2.1 (8).

The sex ratio in dairy goats is distinctly aberrant because of the large numbers of pseudohermaphrodites which are produced. One set of data gave 53.4 per cent males, but the incidence of pseudohermaphroditism was not recorded. In one Saanen herd in which the incidence was high the sex ratio was 49.3 per cent males, 39.6 per cent females, and 11.0 per cent pseudohermaphrodites. A Toggenburg herd gave 46.4 per cent males, 47.6 per cent females, and 6.0 per cent pseudohermaphrodites. A collection of data from Saanen breeders who had many pseudohermaphrodites in their herds gave 55.1 per cent males, 30.0 per cent females, and 14.9 per cent pseudohermaphrodites (9). The pseudohermaphrodites, despite the fact that they possess testes, are therefore reversed genetic females according to sex ratio data (10). Possibly cytological studies of the chromosomes in these aberrant animals might be enlightening.

The pseudohermaphrodite has been often recorded in the literature. Testes are present in all cases, though the tubular and external genitalia present a wide variety of forms in which many gradations appear (11). An analysis of all the cases reported might yield information of interest from the embryological point of view. The condition appears to be inherited as a simple recessive (12), and it is connected in some way with hornlessness, which is inherited as a dominant, since horned hermaphrodites are extremely rare if they occur at all (10,13).

True hermaphrodites are found among goats, and, while rare, they occur with greater frequency than in any other species except, perhaps, the pig.

The sex ratio in the Angora goat, in which pseudohermaphroditism seems to be absent, is 50.1 per cent males, but there is a very high incidence of ridglings (males with an undescended testis), about 5.5 per cent (14). These appear to be genetic males, as the sex ratio is normal if they are counted as such. In the majority of cases only one testis, almost always the right, has failed to descend. The condition is inherited (14).

The duration of gestation in the goat is similar to that in the sheep. A large series of goats of several breeds gave a mean of 150.807 ± .003 days, with a standard deviation of 3.26 days. The modal distribution was 151 days, and 86 per cent fell between 147 and 155 days (15). Some breed differences exist and are recorded in table 18. The month of conception has some influence on the length of pregnancy; it averages 151.3 ± .1 days for August conceptions, and 149.8 ± .1 days for February conceptions. The difference is small, and it might be due to seasonal differences in the length of the heat period, if these exist, since the length is measured from the day of service and not from ovulation. The change between these months is fairly orderly. The age of the dam has some influence on the duration. It is least, 150.1 ± .1 days, when the goat conceives in her first year, as a kid; in the second year it is 150.61 ± 0.6 days; and it gradually rises to a maximum of 151.3 ± .1 days at 6 years. Differences with litter size are not statistically significant (15).

TABLE 17. Average Number of Kids per Birth

BREED	NUMBER OF KIDS
Toggenburg (12)	1.8
Saanen (12)	1.9
Anglo-Nubian (15)	2.1

TABLE 18. Breed Differences in the Duration of Gestation in Goats

BREED	DURATION OF GESTATION, DAYS
Bar Bari (5)	146
Angora (1)	148.08 ± .09
Philippine goats (7)	148.1 ± .07
Jumna Pari (5)	150
Anglo-Nubian (15)	150.0 ± .1
Schwartzwald (16)	150.8 ± .2

PHYSIOLOGY OF THE FEMALE TRACT

Adrenalin causes the muscles of the cornua uteri to relax and the cervix to contract during pregnancy. The cornua are sensitive to oxytocin, but the cervix is not (17).

The urine of the pregnant doe contains 500 to 1,000 M.U. of estrogen per liter from the seventy-fifth to the one hundredth day (18). Removal of the corpora lutea during mid and late pregnancy has invariably resulted in abortion (19).

The breeding season can be changed by modifying the amount of daylight to which the doe is exposed. By increasing the daily amount of light by 1 hour each 10 days after January 25, cycles are said to have ceased prematurely, though it must be remembered that reproductive intensity is normally at a low ebb at this time. By decreasing it by 1 hour a week from April to July, heat was induced in May and June in 3 of 6 does, though breeding was unsuccessful; but in July, after their return to normal light, 4 became pregnant in the first 10 days (20).

A single injection of 400 R.U. of pregnant mares' serum given during anestrum causes the does to come in heat. Priming, which was found necessary in the sheep, is unnecessary. A dose of 200 R.U. is insufficient to produce this effect. Lactating does probably need more P.M.S. to bring them in heat than do dry ones. Several pregnancies resulted from services during the induced heat (2).

THE MALE

The average ejaculate of semen into an artificial vagina is lower for the goat than it is for the ram. For dairy goats it was found to be 0.57 cc., with a range of 0.10 to 1.25 cc. (21); and for Angoras it was 0.66 cc. (1). The sperm content is high, 3 to 4 million per cu. mm. have been reported for Angora bucks (1,22).

There is some evidence that the beard is inherited in a sex-limited manner; the gene appears to be dominant in the male and recessive in the female (23).

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RUPICAPRINAE

Rupicapra rupicapra L.

CHAMOIS

The breeding season of the chamois is said to be in September, and at this time the throat of the male swells (1). In the London Zoo, however, the postcornual scent glands only begin to enlarge during the latter half of September. They reach their maximum size in November and the first half of December and are fully reduced by the end of the first week of January. They do not enlarge in the female (2). The period of gestation has been variously reported from 153 to 210 days.

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ANTILOPINAE

Boselaphus tragocamelus Pallas

NILGAI

This Indian antelope is said to have no regular breeding season in the wild. It breeds immediately after dropping its calves (1). The period of gestation has been observed to be 8 months and 7 days (2). In captivity it experiences a series of diestrous cycles from March to May, each lasting 3 weeks (3). In England, at Woburn, it breeds from March to May (4).

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Other BOVIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Bos (Bison) bonasus L. Wisent				276 days	Europe
Bos (Bubalis) depressicornis H. Smith Anoa				276–315 days	E. Asia
Ovis musimon Schreber Mouflon	Seasonally polyestrous (Heape)			150 days	Zoos
O. vignei Blyth Urial	Sept.–Dec. (Blanford)			180 days	Breeds earlier in Punjab than in Astor
Ammotragus lervia Pallas Barbary Sheep, Aoudad	Monestrous (Heape)			154–161 days	Zoos

Other BOVIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Pseudois nahoor Hodgson Bharal	Monestrous (Prjewalsky). Jan. (Wallace)	May		160 days	Zoos and Mongolia
Capra falconeri Wagner Markhor	Probably monestrous in wild, Dec. (Lydekker)	May–June (Blanford)	1–2	153 days	Himalayas
C. ibex L. Alpine Ibex	Probably monestrous (Heape)			150–180 days	S. Europe
C. pyrenaica Schinz Spanish Ibex		Late Apr. to early May (Lydekker)		At least 20 weeks, probably more	
C. siberica Meyer Asiatic Ibex	Nov.–Dec. (Heape)	May–June (Lydekker)	1–2		Himalayas
Hemitragus hylocrius Ogilby Nilgiri Wild Goat	Most of year (Blanford)		Usually 2		India
H. jemlahicus H. Smith Tahr	Probably monestrous, Dec. (Lydekker)	June–July	1	180 days	Himalayas
Capricornis sumatrensis Bechstein Serow		Sept.–Oct.	1	8 months	Burma. Preorbital glands of male more active in spring (Hodgson)
Nemorhaedus goral Hardwicke Goral		May–June (Blanford)	1	6 months	Himalayas

Other BOVIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Budorcas bedfordi Thomas Takin	End July to early Aug. (Wallace)	End March to early Apr.	Usually 1		China
Oreamnos americanus Blainville Rocky Mountain Goat				147 days	Postcornual glands conspicuous Oct.–Nov. Rocky Mountains
Ovibos moschatus Zimmermann Musk Ox	Aug. (Howe)	Apr.–May	1, twins very exceptional		Arctic America
Alcelaphus buselaphus Pallas Hartebeest	No definite season (Roosevelt and Heller)				S. Africa
A. caama Cuvier Cape Hartebeest	Sept.–Nov. (Bryden)	Oct.–Nov. in S.W. Africa		242 days	Inconsistent. S. Africa
A. lichtensteinii Peters Lichtenstein's Hartebeest	Early summer (S. Hamilton)	Sept.–Nov. (Shortridge)		about 8 months	Cent. Africa
Connochoetes gnu Zimmermann Black Wildebeest, White-tailed Gnu	March (Millais)	Nov.–Jan., usually Dec. (Sclater)	1	8–8½ months	Female breeds before 2 years old. S. Africa
C. taurinus Burchell Blue Wildebeest, Brindled Gnu	June. Not more than 2 cycles in season in captivity (Heape)	Mostly Nov., but range is Sept.–Jan.		8–9 months	Cent. and S. Africa
Damaliscus albifrons Burchell Blesbok				235 days	S. Africa

Other BOVIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
D. lunatus Burchell Sassaby		Sept.–Oct. (Shortridge)		7½–8 months	S. Africa
D. pygargus Pallas Bontebok		Sept.–Oct. (Fitzsimons)		230 days	S. Africa
Cephalophus caerulus H. Smith Blue Duiker		Usually Sept.–Oct. but drops calves all year (Fitzsimons)	1		Africa
C. dorsalis Gray Bay Duiker					In London Zoo, preorbital glands of male markedly swollen in summer (Pocock)
C. natalensis A. Smith Red Duiker		Oct.–Nov. (Fitzsimons)	1, rarely 2		
Sylvicapra grimmia L. Cape Duiker	All year (Fitzsimons)	Mostly early spring and summer	1 occasionally 2	About 4 months	In London Zoo preorbital glands of male discharge in July, inactive in Aug. (Pocock)
Oreotragus oreotragus Zimmermann Klipspringer	Probably extended	Mostly Sept.–Jan. (S. Hamilton)		214 days	Cent. and S. Africa
Nesotragus livingstonianus Kirk Livingstone's Suni		Mid-Nov. to mid-Dec. (Fitzsimons)			Cent. Africa

Other BOVIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Ourebia ourebia Zimmermann Oribi		Sept.–Dec., mostly Dec. (Kirby)		About 7 months	Cent. and S. Africa
Raphicerus campestris Thunberg Steinbok	May have 2 young in a year (S. Hamilton)	Usually summer and fall	1, sometimes 2	7 months	Cent. and S. Africa
R. sharpei Thomas Sharpe's Steinbok		Usually at beginning of rains (Kirby)			Cent. and S. Africa
Adenota vardonii Livingstone Puku		Nov.–Dec. (Selous)			Cent. Africa
Kobus defassa Rüppell Defassa Waterbuck	Probably no regular season (Roosevelt and Heller)	Aug.–Feb., mostly Nov.–Dec.	1		Africa
K. ellipsiprymnus Ogilby Common Waterbuck	Series of 3 weekly cycles, May–July in captivity (Heape)	Sept.–Feb.	1	About 8 months	Cent. Africa
Onotragus leche Gray Lechwe Kob		Aug.–Nov., mostly Oct.		7 months	Cent. and S. Africa
Pelea capreolus Bechstein Vaal Rhebok		Nov.–Dec. (Fitzsimons)	1–2		S. Africa
Redunca arundinum Boddaert Reedbuck	No regular season	Aug.–May		7¾ months	Tends to calve late in summer on mountain plateaus (Fitzsimons) Cent. and S. Africa

Other BOVIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
R. fulvorufula Afzelius Mountain Reedbuck		Oct.–Dec. (Sclater)			Cent. and S. Africa
Aepyceros melampus Lichtenstein Impalla	Apr. to mid-May (Fitzsimons)	Oct.–Dec.	1, twins rare	$6\frac{1}{2}$–7 months	Cent. and S. Africa
Pantholops hodgsoni Hodgson Tibetan Antelope	Winter (Blanford)		1	6 months	Tibet
Antidorcas marsupialis Zimmermann Springbok	Probably somewhat extended	Aug.–Jan., mainly Nov.	1, occasionally 2	171 days	S. Africa. A young castrated male developed slender horns of adult female (Fitzsimons)
Antilope cervicapra L. Blackbuck	Any time, mainly Feb.–March		1–2	6 months	India. In a castrated male the preorbital glands retrogressed to the degree of an immature male (Bennett)
Gazella bennetti Sykes Indian Gazelle	No regular season (Brander)		1–2		N.W. and Cent. India
G. dorcas L. Dorcas' Gazelle	2–3 diestrous cycles in season (Heape)				N. Africa
G. grantii Brooke Grant's Gazelle	No fixed season (Roosevelt and Heller)		1		Cent. Africa

Other BOVIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
G. gutterosa Pallas Seren		June (Wallace)	Usually 2		Neck swells in mating season. China
G. przewalskii Büchner		May (Wallace)			China
G. rufifrons Gray Red-fronted Gazelle					Preorbital glands of male markedly swollen in summer, London Zoo (Pocock)
G. thomsonii Günther Thomson's Gazelle	All year (Roosevelt and Heller)		1–2		Cent. Africa
Hippotragus equinus Desmarest Roan antelope	Apparently no fixed season	Aug.–Feb., mostly Jan.–Feb. in south			Cent. and S. Africa
H. niger Harris Sable Antelope	Apparently no fixed season	Aug.–Feb., mostly Jan.–Feb. in south		270–281 days (observed)	Cent. and S. Africa
Oryx beisa Rüppell Beisa Oryx		Sept. (Roosevelt and Heller)	1	260–300 days	Cent. Africa
O. gazella L. Gemsbok		Oct.–Jan.			Cent. and S. Africa
Strepsiceros imberbis Blyth Lesser Kudu			1		Cent. Africa
S. strepsiceros Pallas Greater Kudu	Apparently no fixed season	Oct.–March		7–8 months	Cent. and S. Africa

Other BOVIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Taurotragus derbianus Gray Giant Eland				260 days	Cent. Africa
T. oryx Pallas Eland	3 weekly cycles, May–July (Heape). Apparently no fixed season in wild	March–Nov.	1	255–70 days	Cent. and S. Africa
Tragelaphus angasi Gray Nyala	Mostly Apr.	Usually Sept.–Oct., sometimes Aug.–March (Fitzsimons)	1		S. Africa
T. scriptus Pallas Harnessed Bushbok	Breeds all year on coast (Sclater)	All year	1	7½ months	Cent. and S. Africa
Tetracerus quadricornis Blainville Four-horned Antelope	In rains (Blanford)	Jan.–Feb.	1–3	183 days	India. Preorbital glands of male very active in summer. (Pocock)
Rhynchotragus kirkii Günther Dik-dik			1		Cent. Africa

PERISSODACTYLA

TOO few species of Perissodactyla have been studied to afford material for generalization. The Equidae all appear to be seasonally polyestrous. In both the horse and the ass the corpus luteum declines early in pregnancy, and gonadotrophins appear in the blood serum. Other changes during pregnancy are noteworthy and have been described in the section on the horse.

RHINOCEROTIDAE

SPECIES	BREEDING SEASON	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Rhinoceros (*Diceros*) *bicornis* L. Black Rhinoceros	No regular season (Roosevelt and Heller); probably Nov.–Dec. (Kirby)	1	530–550 days	Africa
R. (*Ceratotherium*) *simus* Burchell White Rhinoceros	All year (Kirby)	1	17–18 months	Africa. Puberty at 4–5 years
R. (*Dicerorhinus*) *sumatrensis* Cuvier Asiatic Two-horned Rhinoceros	July–Oct.	1	7 months	Sumatra. Puberty at about 20 years (Thorn)

EQUIDAE

Equus caballus L.

HORSE

The horse is seasonally polyestrous, with heat periods commencing early in the spring and continuing, if unbred, well into the summer. The periods are very variable in length, averaging about 22 days, with a heat lasting about 7 days. Ovulation is spontaneous, and it occurs toward the end of heat. The mare has a very high F.S.H. content of the anterior pituitary, higher than that in any other domestic animal. One young is usually born at a time, and twinning very frequently results in abortion. The period of gestation is about 330 days, but seasonal or feed factors cause great variation, more so than in any other species. Histological changes in the reproductive tract are not very marked during the cycle. Ovulation occurs from a restricted portion of the surface of the ovary known as the ovulation fossa. The time of service within the heat period has a great influence upon the chance of conception; the later it occurs, the greater is the chance.

THE ESTROUS CYCLE

The seasonal cycles begin about March and usually continue, in the unbred mare, into August, but many will breed in the fall and winter in England. It is said that in the tropics 2 well-defined breeding seasons tend to occur (1). The length of the cycle is very variable, and the means given (see table 19) vary from 19 to 22¾ days. From the data it is impossible to draw the conclusion, as some have done, that heavier mares have a longer cycle than light ones; more extensive data gathered under comparable conditions are needed to settle the point. The duration of the heat period is also very variable, and the averages range from 4½ to 9 days; but a great deal depends upon the method of testing for heat and on the statistical analysis of the data, since the mare is apt to go out of heat for a short period and to come in again during what is evidently one full heat period (2). The length of life of the corpus luteum appears to be about 15 to 17 days, and one set of data in which the coefficients of variation are given shows that the length of the heat period

is about twice as variable as that of the interval between heats (3). A similar calculation of another set of data (2) gives a C.V. of 49 for the heat period, and of 26.4 for the interval between heats. Thus, the corpus luteum has a relatively constant length of life in the mare. It is said that heat is 1 day shorter if the mare is suckling, and that it tends to be 1½ days longer in March, at the beginning of the season, than in July. There is no constant difference with age or breed (4).

Whatever the length of heat, ovulation bears a closer relation to its end than to its beginning. The symptoms of heat begin to decrease 6 to 12 hours after rupture of the follicle (5), and this, i.e., rupture, occurs in Korean mares about 1.6 days before heat totally ceases (6). It has been found also that 76 per cent of all corpora lutea are first detected from the day before to the day

TABLE 19. Length of the Estrous Cycle in the Mare

	LENGTH OF CYCLE, DAYS			LENGTH OF ESTRUS, DAYS		
	Mean	Standard Deviation	Range	Mean	Standard Deviation	Range
Heavy mares (7)	19.1			$7.0 \pm .16$	2.22	2–16
Belgian draft (8)	20.1		Mode 20, 60 per cent 18–22	5.2		Mode 5, 1–14
Thorobreds (9)	$20.3 \pm .5$	7.5	78 per cent 13–25	$4.96 \pm .13$	2.47	Most 4–7
Percherons (3)	20.94				5.00	
Percherons (10)	21.4				8.9	
Light (8)	22.0		Mode 19, 60 per cent 18–21	5.5		Mode 3, 1–37
Mixed breeds (11)	22.52		56 per cent 19–24	$4.52 \pm .04$		73 per cent 1–5
Semiwild Korean (4)	$22.86 \pm .33$	2.78		$8.98 \pm .25$	2.68	Mode 10
Thorobreds, etc. (4)	$22.79 \pm .12$	4.44		7.53	2.53	Mode 6–8

after heat ceases. These figures apply to Belgian and grade Thorobred mares (2). If the graafian follicle is ruptured artificially on the second day of heat, no corpus luteum is formed, and a new heat begins in a few days. On the other hand, artificial rupture on the fifth day is followed by corpus luteum formation, and the next heat period occurs at the usual time (12). This may demonstrate the importance of the maturation process in preparing the granulosa cells to luteinize, or it may mean that the pituitary is not able to secrete luteinizing hormone early in estrus.

Various anomalies in the heat period, such as the split estrus already mentioned, physiological estrus in which the usual anatomical changes occur but not the psychological state of receptivity, and ovulation after the cessation of heat, have been described (13).

Breeding has no effect upon the length of heat nor upon the time of ovulation (11,14). The left ovary functions more frequently than the right. In a series of 185 ovulations 61 per cent were from the left (2).

The "foal" heat follows soon after parturition, and the mean interval has been given as $9.13 \pm .05$ (11), $9.7 \pm .3$ (7), 11.3 (3), and 11.4 (8) days. It has begun in 75 per cent of cases by the fourteenth day after foaling (8).

The notorious infertility of mares has raised the question of the relationship of the time of service to ovulation. In a long heat period can the spermatozoa deposited early survive until ovulation has occurred? There is a tendency for services early in the heat period to be less successful than those made later, though mid-heat appears to be the best time. One record gives 29 per cent fertility on the first day of heat against 45 per cent on the second to fourth days (15). Another record gives practically no difference on the first 3 days of heat and after that a falling off (16). Neither of these trials takes into account the lengths of the individual heat periods. In a study in which this was considered there was no fertility from services earlier than 7 days before the end of heat, 75 per cent success at 4 days before, and later than that a reduction (17). Insemination prior to ovulation was 86 per cent successful; at the time of ovulation, 74 per cent; and 2 to 10 hours after ovulation, 30 per cent (18). Successes have even been reported if insemination was delayed to 12 to 14 hours after ovulation (19). Another report gives no success 2 to 4 hours after ovulation (20), but it seems that in some cases the egg can be fertilized for at least 20 hours after it has been shed.

The time required for the passage of the egg through the oviduct was found in the case of one mare artificially ovulated by means of pregnancy urine

to be 96 hours. This ovum was found in the last part of the oviduct (21).

Double ovulations, i.e., the rupture of more than one follicle in a heat period, have been observed in 3.8 per cent of cases (2), and twin pregnancies in 3.2 per cent (22) and 1.6 per cent (23). In the first instance only 0.5 per cent twins were born, the remainder were aborted or one of the twins died; and in the second, two thirds terminated in abortion or miscarriage. A report of English Thorobreds in Russia gives 5 per cent of twin conceptions and 1 per cent births, and also records that two thirds of the sets of twins born are of opposite sexes (24). This report also states that the average incidence of twin births in general is 0.57 per cent. A very extensive series gives 1.5 per cent of twin births (25); another, 1.1 per cent (26); and another, 1.23 per cent (27). Evidently the mare is unable, as a rule, to carry twins through gestation.

The sex ratio of the horse at birth has been extensively studied, and the literature has been reviewed in a paper dealing with the sex ratio of hybrids. This work points out that most of the earlier data, obtained from stud books, give a ratio of less than equality, $49.69 \pm .002$ per cent males, in a series of more than a million records. A summary of records obtained from experiment stations gave $52.52 \pm .95$ per cent males, so the ratio is probably a little above equality and similar to that found in other species (26).

The duration of gestation is extremely variable, with breed averages ranging from 329 to 345 days; the standard deviation is usually about 9.5 days. There is a tendency for the lighter breeds to have the longer gestation; hence the saddle horses tend to carry their foals longer than the draft horses (see table 20). There is general agreement that a gestation terminating in the winter is about 20 days shorter than one ending in spring, a surprising difference. Gestations ending in fall and summer are a little shorter than those ending in spring. Males tend to be carried 1.6 to 2.0 days longer than females, and twins 10 days less than singles. Age has little effect, but the gestation period tends to be slightly shorter between the ages of 11 and 13 years (27). A mare carrying a mule foal tends to have a period 10 days longer than she would have had if she had been served by a stallion of her own breed (28,29). This is a little less than midway between the periods of the horse and ass. As the reduction in an ass carrying a hinney is about the same, it suggests a maternal influence on the length of gestation, since if the difference were due to the inheritance of the hybrid, each gestation should be midway between those of the parents.

HISTOLOGY OF THE FEMALE TRACT

OVARY. The ovary of the mare presents several interesting features, one of which is the ovulation fossa, or groove, from which the eggs are liberated. Another is its hypertrophy in the fetus during gestation, and another, the limited life of the corpus luteum during pregnancy. At birth the ovary weighs about 20 g., and at this time a great deal of the interstitial tissue which develops in the fetal ovary has undergone lipid degeneration (34). Graafian follicles are fully formed and the filly usually comes in heat for the first time at about 11 months of age (2). Eight to nine large follicles are produced at each cycle, as a rule, but only one normally ruptures; the rest undergo degeneration (14). The weight of the mature resting ovary is about 40 to 70 g.; it is largest at 3 to 4 years of age, and then gradually diminishes (35).

The ovary of the young mare is much like that of other mammals, with the follicles distributed over the whole ovary. The poles, however, grow inward toward each other, and the ovary becomes covered by a serous coat, leaving only the groove between the poles in which ovulation can occur. This is the ovulation fossa. Small follicles and ova are distributed throughout the stroma, but they migrate to the fossa as they mature (36).

The maturing follicles are from 1 to 3 cm. in diameter at the beginning of heat, and the one which will rupture rapidly grows to about 5 to 6 cm. Palpation of follicles is fairly easy as they are large in relation to the rest of the ovary, but they cannot usually be detected until 1 to 2 days before the beginning of heat (2). During heat the ovary becomes intensely congested, a condition which may be felt as a softening of the stroma (14), but the follicles themselves are tense, even on the first day (2).

Ovulation is spontaneous and is accompanied by a breakdown of blood vessels and considerable bleeding into the cavity. The corpus luteum rapidly forms and is buff-colored when it is new. It persists for 2 to 3 cycles but can be distinguished from the latest one by its darker color. When it is fresh, secondary liquor folliculi is found at the center (35). It is pear- or toadstool-shaped with the stem toward the fossa, and in diameter it is one half to three fourths times that of the follicle (14).

VULVA AND VAGINA. The mucous membranes of the labia, vagina, and cervix become more intensely pink during heat, and congestion is more marked, but the best diagnostic sign is the moist and glistening appearance of the vaginal mucosa at the time of heat. This passes off rapidly after ovulation (37).

TABLE 20. Duration of Gestation in Horses

BREED	DURATION OF GESTATION, DAYS	STANDARD DEVIATION, DAYS
Nonnius (30)	328.9 ± .16	9.5
Rhein-Belgian (31)	332.6 ± .2	7.2
Tragkenen (25)	332.7 ± .07	9.3
Warmblood (25)	332.8 ± .15	9.4
Clydesdale (31)	332.8 ± .9	10.5
Coldblood (25)	333.0 ± .5	9.4
Shire (31)	333.1 ± .9	9.4
Belgian (28)	333.8	
Lippiza (27)	334.3 ± .6	
Lippiza (32)	335.5	
Nonnius (27)	335.9	
Gidrau (27)	336.8	
Thorobred (28)	337.7	
Arab (27)	338.3	
Percheron (31)	342.2 ± .4	10.57
Belgian (33)	344.7 ± .3	
Kladruber (28)	345.4	
Kladruber (31)	345.4 ± .3	9.04

The growth of the vaginal epithelium is not so cyclical in nature in the horse as it is in many species. Mitoses may be found at any time, but they are most frequent during heat. Cornified cells tend to increase in number at this time, but as a layer they are never very prominent. The polyhedral cells of the mid-epithelial zone are largest during heat and smallest at 5 to 10 days of diestrum. Leucocytes are present at all times, but they are most numerous during heat and are least so at 5 to 10 days of diestrum (2).

The vaginal smear is indefinite, as would be expected from the epithelial changes. It is most abundant during heat, and at that time the cornified cells tend to increase, but none of the cellular changes are constant enough to be of diagnostic value (2,38,39,40). The amount of mucus begins to increase 1 to 2 days before heat, the increase continues to ovulation, and at the same time its viscosity is lowered. The volume is lowest and the viscosity is greatest at 5 to 10 days of diestrum (2).

UTERUS. There is no well-marked cervical canal, but the os uteri is well defined, with large folds on the ventral side and a powerful sphincter muscle. There are no tubular glands in the cervix, but epithelial mucous cells are abundant. The os uteri is partly open during the second half of the heat

period, and at this time the mucous cells are swollen. Two days after ovulation these cells have become cubical, but they still contain a fair amount of mucus. At 8 days postestrum there is little secretion, and the subepithelial layer of blood vessels has become reduced. At the beginning of heat the cells lengthen, more secretion is present, the connective tissue becomes looser, the blood vessels increase in number, and many leucocytes invade the cervix (35).

The uterine mucosa is brownish yellow to pinkish yellow. The muscle layers merge into each other, and the long, tubular glands are more numerous in the horns than in the body of the uterus. The connective tissue tends to be loose, with large lymph spaces. The uterine cells are not ciliated. Changes during the cycle are minor only. The uterus is turgid at the beginning of heat, and flaccid toward the end (35). The epithelium is highest during the later stages of heat and at 5 to 8 days of postestrum. On the first day of heat the cells are columnar with some pseudostratification, a condition which increases throughout heat. Minor changes only occur in the glands; they are most active late in heat and at 5 to 8 days postestrum, and least so between these times. The cells are highest and the diameter of the glands is greatest, at 5 days postestrum. Leucocytes are present at all times (2).

OVIDUCT. The oviducts are 30 to 70 mm. long, and are 4 to 8 mm. thick at the ampulla and 2 to 3 mm. thick at the uterine end. They have a dense muscular coat and very many mucosal folds. The subepithelial capillaries are small 2 days before heat and enlarge throughout that period. In diestrum the epithelial cells are cubical, but during heat they become columnar and are filled with secretion. Leucocytes invade the stroma in the heat period (35).

PHYSIOLOGY OF THE FEMALE TRACT

As was mentioned above, the vaginal mucus is most abundant during heat. The pH of this mucus is 8.15 on the first day and 7.9 on the last day of estrus. Corresponding figures for the cervical mucus are 7.75 and 7.85 (2).

The amount of estrogen in the liquor folliculi has been studied in follicles ranging from 1 cm. to 5.5 cm. in diameter. The fluid is aspirated fairly easily from the follicles by a hypodermic needle inserted through the rectum. The amount of estrogen in a follicle varies with its volume, but the quantity per 100 cc. remains about the same regardless of the volume. The results found vary from 2,030 to 2,625 R.U. per 100 cc. The pH of the liquor folliculi varies from 7.6 to 8.1, and it tends to rise with the size of the follicle. The

excretion of estrogens in the urine rises during and just following heat. There is evidence of two peaks, one during heat and one at 10 to 15 days postestrum (41), the latter of which may be related to the decline of the corpus luteum. It is noteworthy that a similar peak has been reported by some workers as occurring in man a short time before menstruation. The decline of the sexual skin in other primates is further evidence that there is a fall in the circulation of estrogens at this time.

The excretion of estrogens during pregnancy can first be detected at from 30 to 40 days, when it is about 250 R.U. per liter. It rises to 17,000 R.U. per liter, or more, at the 260th day, after which the quantity rapidly falls as pregnancy nears its end (42).

The mare is remarkable in that her blood serum contains at a certain stage of pregnancy large quantities of a gonadotrophic hormone (P.M.S.). This first appears at about the thirtieth day, is at a maximum at 45 days, remains high to 115 days, then rapidly declines and cannot be detected after 160 days (42–46). At its peak 50,000 R.U. per liter, or more, are present in the serum. It appears to be formed in the tissue comprising the endometrial cups (47). It is found in the highest concentration in the smaller breeds of mares and may be four times as high in Welsh ponies as it is in draft mares (48). This gonadotrophin has been the subject of considerable study, but authorities are not yet agreed as to its nature, whether it is a single substance or a mixture. It stimulates the ovaries when it is injected into other animals, and the stimulation is mainly follicular, resembling that of F.S.H., but it also has some luteinizing properties (49,50).

Other peculiar phenomena occurring during pregnancy may be related to the appearance of this substance. At about the thirty-fifth day the corpora lutea of pregnancy degenerate. They are followed by a large crop of corpora lutea which, in their turn, degenerate by 150 days. These are formed partly by direct luteinization and partly by the rupture of follicles (51), though some of them appear to be formed by the luteinization of theca interna cells with degeneration of the ovum and granulosa. They are a rich source of progesterone. After 150 days the ovaries become atrophic and fibrotic (52). These organs may be removed at 200 days without interruption of the pregnancy. After the operation estrogen excretion falls but it soon rises again to its normal level, and it is maintained within the normal range for the remainder of the pregnancy (53).

The ovaries of female fetuses from 5 to 9 months after conception weigh 120 to 150 g., compared with 20 g. at birth. During this time they are almost

a solid mass of interstitial cells (34). Fetal testes follow a similar curve of growth and decline (54) and contain large islands of interstitial tissue. These increases occur at the time when the maternal ovaries are devoid of lutein tissue. These fetal gonads do not contain detectable amounts of progesterone, but estrogens are present in a fairly high concentration (34).

The general relationship is, therefore, that the corpus luteum of pregnancy degenerates as serum gonadotrophin appears. The latter apparently causes

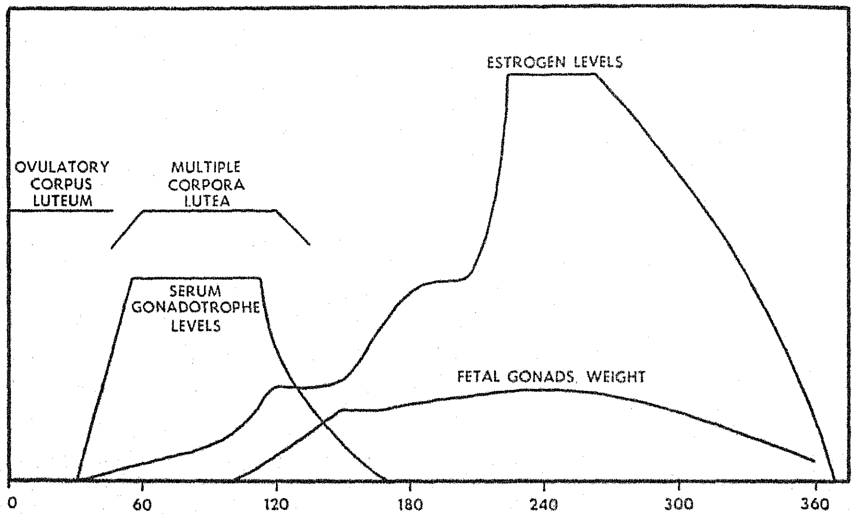

FIG. 1. Diagram of events during gestation in the mare.

new corpora lutea to form. When the serum gonadotrophin disappears, these corpora lutea degenerate and the maternal ovaries become inactive. The fetal gonads now increase enormously in size and remain large until near the end of pregnancy, but there is no evidence that they have taken over the functions of the maternal ovaries. The growth and decline of the fetal gonads correspond with changes in estrogen excretion in the mother's urine. It would be interesting to know whether their growth and decline are associated with changes in the kind and quantity of gonadotrophic hormones in the fetal pituitaries, especially as the reaction resembles a response to the luteinizing hormone.

The anterior pituitary of the adult horse is exceptionally high in F.S.H., but is somewhat low in L.H. content (55). Pituitaries of old mares and old geldings have a strong F.S.H. effect when they are implanted into immature

rats, while stallions' pituitaries give a less strong F.S.H. effect. Young non-pregnant mares and young geldings give an L.H. effect, but that given by the pituitaries of colts and fetuses is mixed. Pituitaries from mares early in pregnancy are low in gonadotrophins. As pregnancy advances their potency rises, followed by a slight decline at about mid-pregnancy (56).

The optimum dose of estrogen to produce heat is 5,000 M.U., and higher doses are less effective. The optimum dose of "prolan" (P.U.) to induce ovulation is 1,000 to 2,000 M.U. (57). At the beginning of heat two injections of 500 M.U. of prolan given at a 5- to 6-hour interval induced ovulation at an average of 44 hours after the first injection. The mares remained in heat an average of 46 hours after ovulation, and the total length of heat was about half the normal time. The injections accelerated the ripening of the follicle and ovulation, and the treated mares were slightly more fertile than untreated ones (58). Pony mares may be ovulated at any time, if moderately large follicles are present, by the injection of 1,000 M.U. of prolan. If this is done during heat, the ovulation occurs 22 to 30 hours after injection and the mare goes out of heat afterwards. If the injections are made outside estrus, ovulation occurs without heat 36 to 60 hours later (21). P.M.S. in doses of 500 to 1,000 M.U. given on 3 to 4 successive days produced heat and ovulation if the injections were made during early or mid-diestrum. It was without effect during anestrum, and so were injections with horse pituitary extract at this time (20).

The size of the living tubal egg is 133 μ, and the zona pellucida is 13.2 μ thick (59).

THE MALE

The ejaculate of the stallion varies from 50 to 200 cc., and the number of spermatozoa varies from 4 to 13 billions. The average ejaculate is about 125 cc., and the average number of spermatozoa is about 8 billion (60). The pH of the semen varies from 6.94 to 7.51, with an average of 7.31 (61). Another observer gives an average pH of 7.23 (62). The spermatozoa are able to travel at the rate of 3 to 4 mm. per minute. They live for less than 6 hours in the vagina and for 12 hours in the uterus, but the data are insufficient for us to be sure that these times are even approximate (61).

A single observation has shown that spermatozoa may remain alive in the male tract for at least 3 weeks as they were found in a stallion gelded for that length of time (63). The length of the epididymis is 72 to 86 metres,

and the number of ejaculatory ducts is 12 to 18 (64). The mean head length of spermatozoa is 6.3 μ (65).

The urine both of the stallion and of the mare contains a large variety of sterols which appear to be metabolic products of the gonadic hormones. Stallions' urine is an exceptionally rich source of estrogens, since that of immature males contains 1,000 to 10,000 M.U. of estrogen per liter, and that of adults, 20,000 to 50,000 M.U. The titer is highest in spring and summer and is lowest during the winter (66).

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Equus asinus L.

ASS, DONKEY

The female ass reaches puberty at one year of age. The breeding season is limited as it is in the horse; some jennets experience cycles from March to August, and some for a longer period. In South Africa the breeding season is from the second half of October to the first half of April (1). The estrous cycle lasts 21 to 28 days, and heat 2 to 7 days (2). The mean cycle is 22 days long, the mean duration of heat is 4.7 days, and ovulation is usually during the last third of the heat period. The foal heat occurs modally 17 to 18 days after parturition, with a spread from 6 to 69 days (3). In Mississippi foal heat sets in 2 to 8 days after foaling and lasts 2 to 6 days; ovulation is approximately 48 hours before the end of heat (2). One young is usually born at a time. The period of gestation is about 365 days, but it is 8 to 12 days less if the jennet is carrying a hinney (4).

The ovaries are relatively small. Follicles are arranged in rows, develop at the cranial pole, and move caudally. There is no ovulation fossa at first; later the polar ends of the ovaries grow disproportionately, curve toward each other, and the ovulation fossa comes into being. Ovulation does not occur at each heat period, especially in younger females. Blood is extravasated in the ruptured follicle, as it is in the mare. The corpus luteum is very inconspicuous at parturition (1), so that one may suspect that the peculiar series of reactions observed in the mare during pregnancy occur also in the jennet.

The labia swell during heat, and at this time blood-stained mucus is produced (1). The vagina during heat contains abundant mucus, which liquefies and flows as heat progresses. The cervix becomes relaxed, flabby, and dark red, and it frequently shows hemorrhagic spots during this period. It is slightly narrower and longer than it is in the mare. It protrudes far into the vagina and is situated close to the floor. In open jennets it is rather tortuous, even during heat, but during the foal heat it is wide open (2).

Gonadotrophins may be detected in the blood from 40 to 200 days of pregnancy (5). On the fiftieth day, 5,000 to 10,000 M.U. per liter have been found, but the level falls too low for accurate pregnancy diagnosis after the 150th to 160th day of gestation (6).

Estrogens can be found in the urine from 50 days of pregnancy onward. At this time about 1,000 M.U. per liter are present. The amount increases to 70,000 M.U. per liter at 101 days; it then decreases but does not fall much below 1,000 M.U. per liter (6).

The volume of semen per ejaculate is from 70 to 115 cc. (7), or 40 to 100 cc. (2). In another report a mean volume of 54 cc. was given (8). The concentration of spermatozoa is from 95 to 264 million per cc. in a group of jacks in which the mean volume was apparently on the low side (8). In species in which a large proportion of the ejaculate comes from the accessory glands the mean number of spermatozoa per unit volume is likely to be very variable. The sperm concentration of jack's semen is higher than that of stallions (2) and the total output at an ejaculation seems to be greater, as it varies from 8 to 21 billions (7).

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Other EQUIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Equus grevyi Oustalet Grevy's Zebra				390 days	No rutting season for males
E. hemionus Pallas Asiatic Wild Ass		June–Aug. (Blanford)			
E. kiang Moorcroft Kiang	Aug.–Sept. (Schafer)	July		365 days	E. Tibet

Other EQUIDAE (*Continued*)

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
E. quagga Gmelin Quagga (Burchell's Zebra)		Apr.–Dec., mainly Aug.–Nov.	1	340–365 days	S. Africa
E. zebra L. Mountain Zebra			1	12 months	

TAPIRIDAE

SPECIES	BREEDING SEASON	SEASON OF BIRTH	NO. OF YOUNG	GESTATION PERIOD	HABITAT, ETC.
Tapirus indicus Desmarest Malay Tapir				390–395 days	Malay Peninsula
T. terrestris L. Brazilian Tapir	Before beginning of rains (Cabrera and Yepes)			397.4 ± 1.2 days	S. America

INDEX OF LATIN NAMES

INDEX OF VERNACULAR NAMES

GENERAL INDEX

Only those species which are the subjects of separate articles have been included in this index. Much more information on breeding seasons, litter size, gestation periods, etc., in other species is included in the unnumbered tables. The Index of Latin Names should be used to find this information.